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A MONOGRAPHIC REVISION OF THE ANT GENUS *LASIUS*

By Edward O. Wilson

Biological Laboratories, Harvard University

With Two Plates

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No. 1 — *A Monographic Revision of the Ant Genus* LASIUS

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INTRODUCTION

Lasius is one of the most prominent and familiar of the Holarctic ant genera. From the time of Réaumur in the eighteenth century (Wheeler, 1926), European and North American entomologists have focused attention on it in countless general biological and taxonomic investigations which are today part of the classical foundation of myrmecology. It is probably best known for its conspicuous nuptial flights, its habit of tending and transporting homopterous insects, and the temporary parasitic behavior of some of its species. It has also attracted much attention as one of the several ant genera which have persisted

in Europe and North America since early Tertiary times with only a small amount of visible evolutionary change.

Today it occupies a purely Holarctic range. Northward it reaches northern Scandinavia, the Baikal region of Siberia, Kamchatka, southeastern Alaska, and southern Labrador. Southward it reaches Madeira, North Africa, northern Iraq, the southern Himalayas, the mountains of Formosa, the mountains of central Mexico, and northern Florida. Where it comes closest geographically to tropical faunas, as in southeastern Asia, it still retains its north-temperate character, i.e., limited to temperate vegetation at higher elevations and there associated chiefly with typically Holarctic ant genera.

Within this range it is among the most abundant of all insect genera. In Europe the two species *niger* and *flavus* are often the overriding dominants of the ant fauna in local situations and under a variety of ecological conditions. In the eastern United States *L. neoniger* (=*L. niger americanus div. auct.*) mounts such dense populations in open fields and lawns that W. M. Wheeler was once moved (1905) to suggest that it might be the most abundant insect in North America. Such a contention would probably be an exaggeration with respect to all insects, of course, yet there is no denying *neoniger* its importance as a major faunal influent within its range and favored habitat.

Despite the great prominence of this genus, the taxonomy of *Lasius,* like that of most ant genera, has been a sorry shambles. In particular, there have been no keys that work satisfactorily; those in the literature today will not suffice to determine even the type specimens of many species. A principal reason for this condition is that some of the best diagnostic characters in the genus involve structures hitherto ignored. Furthermore, the nomenclature has been badly complicated by an excessive accumulation of poorly defined forms, mostly of a trivial infraspecific nature. Out of the 110 unchallenged names which existed in the literature at the outset of this revision, I have been able to establish only 27 as representing valid species (not counting the six additional new species). The others patently serve only to obscure the true picture of intraspecific variation and to render clearcut species diagnoses impossible. Finally, the situation has been aggravated by the hitherto unsuspected presence

of a number of cryptic species closely related to some of the most common members of the genus. Formerly lumped with their named siblings, they have had the effect of broadening and confusing species diagnoses. Creighton (1950), for instance, recognizes only two forms of the subgenus *Lasius* in North America, "*niger neoniger*" and "*alienus americanus*", which he and others have separated principally by a single character in pilosity. Actually, these two names apply to six distinct species in North America: *sitkaensis* Pergande, *niger* (Linnaeus), *alienus* (Foerster), *neoniger* Emery, *crypticus* Wilson, and *sitiens* Wilson, each abundant and widely distributed. It is impossible to make a two-way split in this group on the basis of the pilosity character, since in this respect *sitkaensis* by itself brackets all of the variation shown by the other species. The taxonomy of the group was finally solved in the course of the present study by reference to other characters in dentition, clypeal outline, etc., combined with trends in pilosity.

Beyond the urgent need for a purely taxonomic revision, *Lasius* has presented many excellent opportunities for studies of more general nature. Chief among its advantages in this respect is the large amount of available material, which has allowed extensive statistical descriptions and analyses. I have been able in the course of only two years to gather and examine an estimated total of 5,425 nest series containing approximately 80,000 specimens. Not every specimen in every nest series was studied microscopically, but all were at least cursorily checked, and contributed to overall impressions of variability in size, color, and habitus. *Lasius* is also remarkable — perhaps unique — among animal groups thus far monographed, in its great abundance, ubiquity, and conspicuousness, and the consequent ease with which it can be found in the field. Anywhere in the northern United States, in practically all but desert and semidesert conditions, it is possible for an investigator to walk onto nearly any plot of ground and within a matter of minutes find nests of one or more species. As a result, surveys of population density and comparative ecology can be conducted swiftly and easily.

REFERENCE COLLECTIONS

During the course of this study collections of *Lasius* from many sources have been handled, and nest series divided and redistributed in such a way as to allow an efficient dispersal of duplicate type and determined material. At the present time the single most important reference collection is that of the Museum of Comparative Zoology of Harvard University. I have made an effort to concentrate here nest duplicates of all of the significant series in this study, including types, and have succeeded in building substantial collections of all but the rarest species. This material will be available to check possible errors in the revision, and will provide a starting point for future studies of a similar nature. Below are listed other institutions and private collections (the latter under the collector's name) which are considered important by virtue of their containing types and critical determined material. They are accompanied by the abbreviations used to designate them in the descriptive parts that follow.

Academy of Natural Sciences, Philadelphia (ANSP).
American Museum of Natural History, New York City (AMNH).
Zoologisches Museum der Universität, Berlin (Berlin Museum).
Mr. Michel Bibikoff, Leamington Spa, England (Bibikoff Coll.).
Bondroit Collection, Institut Royal d'Histoire Naturelle de Belgique, Brussels (Bondroit Coll.).
British Museum (Natural History), London.
California Academy of Sciences, San Francisco (CAS).
Dr. A. C. Cole, University of Tennessee, Knoxville (Cole Coll).
Dr. W. S. Creighton, City College of New York (Creighton Coll.).
Emery Collection, Museo Civico di Storia Naturale, Genoa (Emery Coll.).
Forel Collection, Muséum d'Histoire Naturelle, Geneva (Forel Coll.).
Docent Karl-Herman Forsslund, Skogsforskningsinstitut, Experimental fältet, Sweden (Forsslund Coll.).
Dr. Holger Holgersen, Stavanger Museum, Stavanger, Norway (Holgersen Coll.).
Illinois State Natural History Survey, Urbana (INHS).
Dr. Robert L. King, University of Iowa, Iowa City (King Coll.).
Dr. Heinrich Kutter, Flawil, Switzerland (Kutter Coll.).
Mayr Collection, Naturhistorisches Museum, Vienna (Mayr Coll.).
Museum of Comparative Zoology, Harvard University, Cambridge, Mass. (MCZ). Includes W. M. Wheeler and B. Finzi Collections.

Mr. H. Okamoto, care of Dr. K. Yasumatsu, address below (Okamoto Coll.).

Santschi Collection, Naturhistorisches Museum, Basel, Switzerland (Santschi Coll.).

Schenck Collection, Zoologisches Museum der Universität, Marburg, Germany.

Snow Entomological Museum, University of Kansas, Lawrence.

Dr. Mary Talbot, Lindenwood Côllege, St. Charles, Missouri (Talbot Coll.).

United States National Museum, Washington, D. C. (USNM).

University of Michigan Museum of Zoology, Ann Arbor (UMMZ).

Dr. N. A. Weber, Swarthmore College, Swarthmore, Pennsylvania (Weber Coll.).

Dr. G. C. Wheeler, University of North Dakota, Grand Forks (G. C. Wheeler Coll.).

W. M. Wheeler Collection, see Museum of Comparative Zoology.

Dr. Keizô Yasumatsu, University of Kyushu, Fukuoka (Yasumatsu Coll.).

ACKNOWLEDGMENTS

This study was made possible by the cooperation of many European, Japanese, and American entomologists who have contributed specimens and ecological information from over the entire range of *Lasius*. It has been primarily through their efforts that I have been able to examine the largest amount of material ever assembled for a revision of any group of ants, and one excelled by few other collections of special insect groups. Professor K. Yasumatsu and Mr. H. Okamoto of Japan made available from their collections what is probably several times over the number of nest series of *Lasius* seen by all non-Japanese myrmecologists in the past. Dr. G. C. Wheeler sent the enormous collection which he and his students have been gathering from the North Dakota area for the past twenty-five years, containing the impressive sum of over 900 nest series and many tens of thousands of individual specimens. Others have lent their personal collections or the institutional collections in their charge to swell by at least tenfold the number of series which were initially available in the Museum of Comparative Zoology and my own collection. Space does not permit me to detail the material and help received from every person; I can only list

their names, along with their addresses or the reference collection with which they are associated, and express to each my sincere appreciation for their cooperation.

Prof. R. H. Beamer (Snow Entomological Museum, University of Kansas); Dr. M. Beier (Mayr Coll.); Mr. Michel Bibikoff (Bibikoff Coll.); Dr. M. V. Brian (The University, Glasgow, Scotland); Dr. H. Bischoff (Berlin Museum); Dr. Charles Bisgaard (Zoologisk Museum, Copenhagen); Dr. W. L. Brown (MCZ); Dr. L. F. Byars (U. S. Public Health Service, Savannah, Georgia); Prof. F. M. Carpenter (MCZ); Dr. Kenneth Christiansen (American University of Beirut, Lebanon); Dr. A. C. Cole (Cole Coll.); Monsieur A. Collart (Bondroit Coll.); Mr. C. A. Collingwood (Evesham, Worcestershire, England); Dr. T. W. Cook (Oakland, California); Dr. W. S. Creighton (Creighton Coll.); Dr. Ch. Ferrière (Forel Coll.); Docent K.-H. Forsslund (Forsslund Coll.); Prof. S. W. Frost (Pennsylvania State University); Mr. N. Gillham (MCZ); Dott. Delfa Guiglia (Emery Coll.); Prof. Ed. Handschin (Santschi Coll.); Dr. Holger Holgersen (Holgersen Coll.); Mr. P. B. Kannowski (UMMZ); Dr. R. L. King (King Coll.); Prof. C. Kosswig (Zoologi Enstitüsü, Müftülük Binasinda, Istanbul); Mr. Kenneth Kraft (University of North Dakota, Grand Forks); Dr. Masao Kubota (Odawara, Kanagawa Pref., Honshu); Dr. Heinrich Kutter (Kutter Coll.); Mr. W. E. LaBerge (University of Kansas, Lawrence); Mr. Borys Malkin (Malkin Coll.); Dr. W. L. Nutting (Biological Laboratories, Harvard University, Cambridge, Massachusetts); Mr. H. Okamoto (Okamoto Coll.); Dr. Fergus J. O'Rourke (University of Cork, Eire); Dr. Orlando Park (Northwestern University, Evanston, Illinois); Dr. Albert Raignier (Institut de Zoologie, Louvain, Belgium); Dr. E. S. Ross (CAS); Dr. M. R. Smith (USNM); Dr. L. J. Stannard (INHS); Dr. Mary Talbot (Talbot Coll.); Mr. Ernest Taylor (Oxford University Museum, England); Mr. B. D. Valentine (Biological Laboratories, Harvard University, Cambridge, Massachusetts); Father Joseph van Boven (Roermond, Holland); Dr. A. F. Van Pelt (Appalachian State Teachers College, Boone, North Carolina); Dr. N. A. Weber (Weber Coll.); Dr. G. C. Wheeler (G. C. Wheeler Coll.); Dr. I. H. H. Yarrow (British Museum); Dr. Keizô Yasumatsu (Yasumatsu Coll.).

In addition, I would like to make special acknowledgments to

two men who in personal contact with the writer have had a major influence in the shaping of this study and deserve a large part of the credit for whatever success it may enjoy. Dr. W. L. Brown has followed the revision step by step and drawn upon his truly great knowledge of ants to help guide the work through its most difficult phases. There are doubtless errors remaining in this work but they are much fewer than in the original drafts thanks to his painstaking and enlightened inquiry into nearly every detail. Prof. F. M. Carpenter has made possible the work on the fossil species by arranging the loan of the Museum of Comparative Zoology collections and directing the writer in their preparation and examination. But he has been even more helpful as my graduate sponsor at Harvard, in which role he has always been most thoughtful and graciously patient.

I would also like to express appreciation to Prof. Ernst Mayr for his effective and penetrating advice on certain matters of taxonomic procedure and theory; to Miss Ruth Dunn for her aid in the translation of Russian scientific papers; to Dr. W. L. Nutting and Mr. Thomas Eisner for aid in field work and preparation of illustrations; and to Miss Janice Cassani for aid in the preparation of the final manuscript.

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GENERIC STATUS AND SUBGENERA

Lasius as originally conceived by Fabricius (1805) contained two species which are recognizable at the present time, *niger* (Linnaeus) and *emarginatus* (Olivier). The generic name *Lasius* was not used consistently, however, until Mayr (1861) revived it and set up the limits recognized today. In 1903 Bingham designated *niger* as the generitype. Some disorder was introduced in 1914 when Morice and Durrant called attention to an early paper by Jurine (1801) in which the name *Lasius* had been proposed for a genus of bees prior to Fabricius' publication. For the ant genus they created the name *Donisthorpea*, with *niger* as the generitype. This unfortunate nomenclatural maneuver precipitated a great deal of debate among ant specialists and began a lengthy period during which several names (*Lasius*, *Acanthomyops*, *Formicina*, *Donisthorpea*) were used for the

genus simultaneously. The historical details have been reviewed by Donisthorpe (1927) and Creighton (1950) and for practical purposes are now largely irrelevant. It is sufficient to say that in 1935 the International Commission of Zoological Nomenclature ruled Jurine's publication invalid and restored *Lasius* to the ants. Among ant taxonomists, in recent years, only Donisthorpe refused to accept this ruling and continued to use the name *Donisthorpea*.

DIAGNOSIS. The species of *Lasius* belong to the subfamily Formicinae, section Euformicinae (*sensu* Emery, 1925). They belong with the group of genera comprising Emery's 1925 concept of the closely related (and possibly inseparable) tribes Lasiini and Formicini. Within the orbit of these genera, *Lasius* can be characterized as follows: Size small to medium; worker and queen bodies robust, with heads massive relative to the alitrunk; palpal segmentation 6, 4 (except in males of *Dendrolasius*, the terminal palpal segments of which exhibit variable and irregular ankylosis); worker and queen mandibles with 7 to 12 teeth following the typical formicine pattern (as defined on p. 000; a single exception is found in the queen of *L. carniolicus*, which has reduced dentition), primitively with one or more offset teeth at the basal angle; male mandible primitively with a narrow preapical cleft, a well defined basal angle, and anterior masticatory denticles; worker alitrunk not conspicuously constricted or otherwise specialized, the mesonotum typically convex in side view; propodeal spiracle round; petiolar scale in side view prominent, erect, and typically symmetrical; male genitalia generalized but weakly developed.

The closest living relative of *Lasius* is the Nearctic genus *Acanthomyops*, which is believed to be a temporary social parasite on some *Lasius* members. *Acanthomyops* differs consistently only in its reduced palpal segmentation (formula—3, 4). In other characters, including habitus and pilosity, it is overlapped by members of the subgenus *Lasius* (*Chthonolasius*), which is most likely its direct ancestor. Beyond this one sound phylogenetic link, the affinities of *Lasius* are difficult to ascertain. The mandible form of its primitive members is the most generalized encountered within the Lasiini and Formicini, and may represent the prototypic condition for the Formicinae as a whole. The genera ordinarily bracketed with *Lasius*—*Prenolepis*,

Paratrechina, and *Pseudolasius* — show considerable modifications in mandibular structure, pilosity, and body form which set them well apart from this genus. On the other hand, *Formica* is generalized in the same characters as *Lasius* and may be closer to it, despite several striking specializations in the male. Future revisionary work will probably necessitate either the incorporation of the Lasiini into the Formicini, or the division of this tribal complex along different lines than those now recognized.

LASIUS Fabricius

Lasius Fabricius, 1805, Systema Piezatorum, p. 415. Generitype: *Formica nigra* L., designated by Bingham, 1903, The Fauna of British India, 2: 338.

Formicina div. auct., nec Shuckard, 1840 (generitype *Formica rufa* L., designated by Wheeler, 1911, Ann. New York Acad. Sci., 21: 164).

Acanthomyops div. auct., nec Mayr, 1862 (generitype *Formica clavigera* Roger, by monotypy), *part.*

Donisthorpea Morice and Durrant, 1914, Trans. Roy. Ent. Soc. London, pp. 421–423. Generitype: *Formica nigra* L., by original designation.

Subgenus LASIUS Fabricius

DIAGNOSIS. Queen non-parasitic, the head width much less than the width of the thorax just in front of the tegulae. Worker eye length at least 0.20 × the head width, and usually more. In all three castes the metapleural gland is not reduced, i.e., the greatest width of the gland opening measured perpendicular to its long axis is greater than the maximum length of the propodeal spiracle, including the darkened rim. Worker body color usually light to blackish brown, rarely yellowish brown. Maxillary palp segments V and VI typically subequal in length to segment IV, and length of segment VI typically exceeding 0.14 × the head width. Male mandible showing interspecific variation from the most primitive type in the genus (*sitkaensis*) to the most advanced (*niger* complex). *Lasius sitiens* Wilson is intermediate to the subgenus *Cautolasius* in its lightened body color, reduced eye size, and shortened terminal maxillary palp segments (length of segment VI 0.12-0.14 × the head width), but these are obviously secondary modifications. The closest relative of *sitiens,*

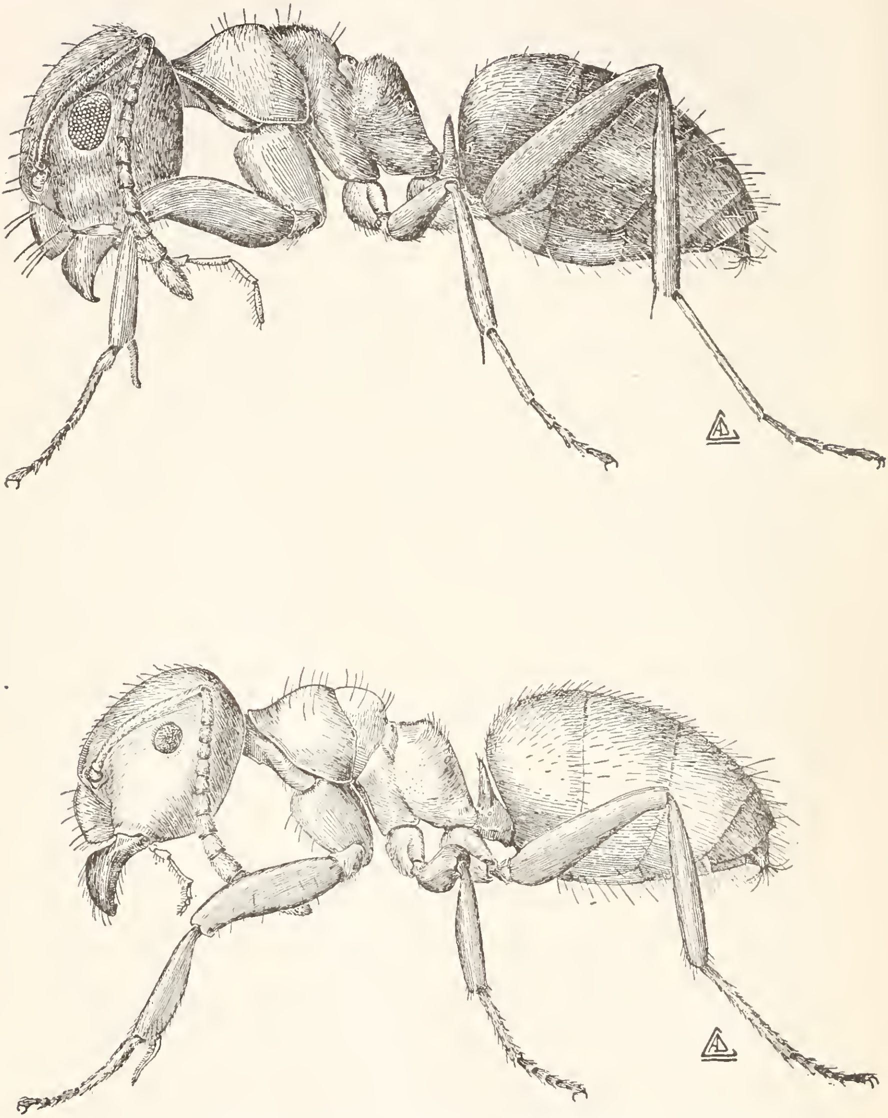


Fig. 1. *Above*, worker of *Lasius* (*Lasius*) *alienus* (Foerster). *Below*, worker of *Lasius* (*Chthonolasius*) *umbratus* (Nylander). Both specimens from North America. Original by A. D. Cushman, courtesy of M. R. Smith.

L. crypticus Wilson, shows a similar shortening of the maxillary palps, and both are connected in this character to the remainder of the subgenus by the more generalized species *L. neoniger* Emery. (See Fig. 1.)

Subgenus CAUTOLASIUS Wilson, new subgenus

Subgeneritype: FORMICA FLAVA Fabricius, by present selection.

I propose to separate the members of the *flavus* complex — *flavus* (Fabricius), *nearcticus* Wheeler, *alienoflavus* Bingham, *talpa* Wilson, and *fallax* Wilson — as a distinct subgenus. This group of species is closely knit and shows a mixture of characters which on purely morphological grounds places it in a position intermediate between *Lasius s. s.* and *Chthonolasius*. The worker caste closely resembles that of *Chthonolasius*, in having light body color, reduced eye size, and shortened maxillary palps. However, these are most likely convergent characters developed in connection with a common subterranean mode of life. The closest affinities of *Cautolasius* are to *Lasius s. s.*, and it was probably derived from the latter subgenus. The queen is non-parasitic and very similar to *Lasius s. s.* in habitus, with the head small relative to the thorax. In all three castes the opening of the metapleural gland is as large as in *Lasius s. s.* Male mandible showing the maximum range of variation for the genus (*sitkaensis* to *niger* types), within a single species (*flavus*). The most primitive member of the subgenus, *L. alienoflavus* Bingham, has terminal maxillary palp segments fully as long as those of *L.* (*L.*) *sitiens* Wilson, while the color variation of *L. flavus* overlaps that of *sitiens*. In final analysis the only character which by itself will separate the two subgenera is eye size. Yet the two still represent discrete groups, since *sitiens* is a secondarily specialized member of a phylogenetically remote species group.

Subgenus CHTHONOLASIUS Ruzsky

Chthonolasius Ruzsky, 1913, Arch. Naturgesch., **79**(A9): 59–61. Subgeneritype: *Formica umbrata* Nylander, by designation of Emery, 1925, Genera Insect., fasc. 183, p. 232.

DIAGNOSIS. Queen temporarily parasitic on species of *Lasius s. s.;* the head width about as great as the width of the

thorax just anterior to the tegulae or greater. Worker eye length never more than 0.17 × the head width and usually less. Metapleural gland reduced in all three castes, so that the gland opening measured perpendicular to the long axis is less than the maximum length of the propodeal spiracle, including the darkened rim. Worker color light yellow to light yellowish brown. Maxillary palp segments V and VI conspicuously reduced relative to IV, the length of VI typically not exceeding 0.10 × the head width. Pilosity often highly specialized, apparently as a parasitic coadaptation. Male mandible of the primitive *sitkaensis* type. The following larval characters have been established in the present study: relative to *Lasius s. s.* (*sitkaensis, alienus*) and *Cautolasius* (*flavus*), the *Chthonolasius* head is more slender and the external mandibular borders more convex (see figures in G. C. Wheeler, 1953, p. 153). (See Fig. 1.)

Subgenus DENDROLASIUS Ruzsky

Dendrolasius Ruzsky, 1913, Arch. Naturgesch., **79**(A9): 59. Generitype by monotypy: *Formica fuliginosa* Latreille.

DIAGNOSIS. Queen head width and worker eye size as in *Chthonolasius*. Metapleural gland reduced in the queen and male and, unlike the other subgenera, lacking guard hairs; yet well developed and with guard hairs in the worker. The scutum of the queen in side view overhangs the pronotum and contributes all of the anterior alitruncal convexity, whereas in the other subgenera it shares the convexity with the pronotum. Worker color jet black. Maxillary palp segments V and VI subequal to IV, but the entire palp reduced in size, so that VI does not exceed in length 0.12 × the head width. Male mandible of the advanced *niger* type.

PHYLOGENY WITHIN THE GENUS

I have represented in the diagram of Figure 2 my own conception of the phylogenetic deployment of the species of *Lasius*. All evidence points to *L. sitkaensis* Pergande, a boreal Nearctic species, as the most generalized member of the genus. First, it carries the characters of the subgenus *Lasius,* which is morphologically and ethologically the most generalized of the four

subgenera. Second, *sitkaensis* possesses characters in the mandible form which appear, both in the female and male, to be end points of independent morphoclines. The offset basal tooth of the female is not shared by any other *Lasius s. s.* or *Cautolasius* (a similar structure of doubtful homology occurs occasionally in the queen of *L. neoniger* Emery, *q. v.*), but it is characteristic

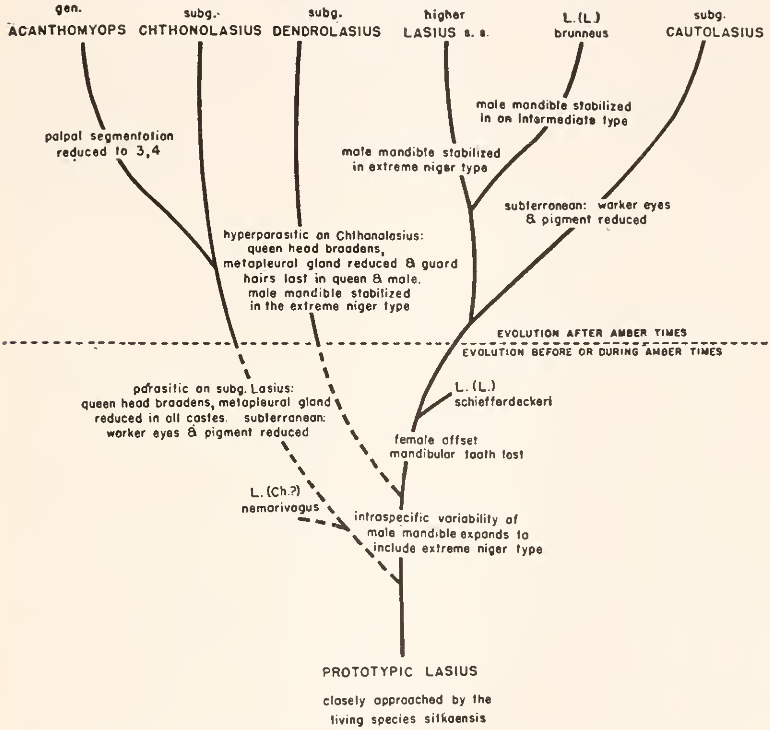


Fig. 2. Phylogeny within *Lasius*. Further explanation in the text.

of *Dendrolasius* and appears sporadically on *L. umbratus* (*Nyl.*), which species is in other characters the most generalized member of *Chthonolasius*. The form of the male mandible ("*sitkaensis* type", p. 37) is shared with *Chthonolasius; Cautolasius* shows within its membership all gradations from this type to the "*niger* type"; *L.* (*L.*) *brunneus* (Latr.) has an intermediate

condition; and *Dendrolasius* and the remainder of living *Lasius* *s. s.* possess the *niger* type. There is some evidence to indicate that the male morphocline, at least, reflects real sequential evolution. The Baltic amber species *L.* (*L.*) *schiefferdeckeri* Mayr has a highly variable male mandible ranging from *sitkaensis* type to an intermediate type, while the Florissant species *L.* (*L.*) *peritulus* (Ckll.) has the advanced *niger* type.

There is a possibility that *L. sitkaensis* has diverged from the generic prototype by an increase in size and acquisition of standing appendage pilosity. The evidence for this is simply that *L. schiefferdeckeri,* which is intermediate between it and the *niger* complex in the crucial structure of the male mandible, is quite small and lacks standing appendage pilosity. Moreover, both characters appear on other grounds to be specialized conditions which have been developed polyphyletically in several sections of the genus.

If the assumption be made that *sitkaensis* does represent a little-changed derivative of the ancestral population, and that the fossil *schiefferdeckeri* represents the prototype of the higher members of the nominate subgenus (for further evidence see under description of this species) then it becomes possible to thread together the evolutionary history of *Lasius s. s.* in plausible zoogeographic terms. According to the hypothesis which I consider to be the simplest and most consistent with past and modern distributions, the *Lasius* prototype, very similar to the living species *sitkaensis,* at one time ranged over both Eurasia and North America. By Baltic Amber times (Oligocene) the Eurasian segment of this population had evolved into *L. schiefferdeckeri,* a type intermediate between *sitkaensis* and the *niger* complex. At least part of the North American segment, and probably all of it, remained static with respect to this morphocline. By Florissant times (lower to middle Oligocene, see MacGinitie, 1953), the *niger* male mandible type had been stabilized in one or more species, and a species possessing it (*L. peritulus*) had invaded North America. In Europe the *niger* complex was undergoing speciation along the lines already foreshadowed by the variability of the ancestral species *schiefferdeckeri,* and the derivative species were in the process of radiating into several major habitats: *brunneus* was mostly arboreal, *alienus* and *emarginatus* showed southern affinities and favored

open, dry situations, and *niger* was more cold-adapted and could penetrate forests in addition to open situations. In North America a different situation prevailed. The old relict species *sitkaensis* was well adapted to the colder forested areas and was not displaced from them by the later *niger* complex invaders. *Alienus*, either the same species as the Florissant *peritulus* or closely related to it, came to occupy the more southern forests. The open habitats were filled with the three species of the *neoniger* complex (*neoniger, crypticus, sitiens*), a specialized group limited to North America and probably derived from an early *niger* complex ancestor. *Niger* itself appears to have reached North America by a later invasion and is today still a relatively uncommon ant limited to the mountains of the western United States.

SOME FINDINGS OF GENERAL THEORETICAL INTEREST

Rate of evolution. Lasius is often cited as a genus with an extremely low rate of evolution. Gustav Mayr (1868) and Wheeler (1914) have stated that the Baltic Amber *L. schiefferdeckeri* Mayr is very little different from the modern siblings *L. niger* (L.) and *L. alienus* (Foerst.) and may be directly ancestral to all the members of the *niger* complex. The present study has included an analysis of this relationship based on a limited collection of amber specimens (see p. 52). *L. schiefferdeckeri* has been shown to differ morphologically from *niger* and other members of the nominate subgenus by about the same amount of difference that separates modern species on the subgenus. As stated previously (under Phylogeny within the Genus) *schiefferdeckeri* appears to be transitional between the hypothetical subgeneric prototype, most closely represented by the living *L. sitkaensis* Pergande, and more advanced species. Moreover, it exhibits variation in the scape index which is transspecific with respect to members of the modern *niger* complex. *L. peritulus* (Ckll.) of the Florissant shales is a true member of the *niger* complex and must be very close to living members such as *L. alienus* (Foerster). Unfortunately, preservation is too poor to allow its specific status to be judged with certainty.

Geographic speciation. There no longer can be any doubt that

geographic speciation, as reflected by phenomena in geographic variation, is operative in the better studied groups of higher animals. There is a growing body of evidence to indicate that it occurs generally in all sexually reproducing animals. Indeed, with the exception of germinal polyploidy, which is rare in animals, it is difficult on theoretical grounds to conceive of any scheme of sympatric speciation which is plausible and consistent with our present knowledge of population genetics. By far the simplest process of speciation would seem to be the geographic isolation of populations and their subsequent divergence to potential reproductive isolation.

Species distributions and infraspecific variation patterns in *Lasius* are entirely consistent with the theory of geographic speciation. There is present within the genus all of the different "stages" that would be expected to occur in this process. These can be summarized sequentially as follows.

(1) The geographic variation is barely detectable. Examples: pilosity and body color in *L. sitkaensis,* eye size in *L. umbratus.*

(2) The geographic variation is stronger, producing (in individual characters) conventional subspecies patterns. Examples: pilosity in *L. niger,* male genitalia in *L. niger* and *L. alienus*, pilosity in *L. fuliginosus.*

(3) The geographic variation is very strong, producing differences between terminal populations exceeding those which separate some sympatric species pairs. Examples: appendage length, eye size, and polymorphism in *L. flavus;* habitat preference and nesting habits in *L. alienus.*

(4) Two populations have attained species status by morphological criteria, but still replace one another geographically. Example: *L. emarginatus* and *L. productus.*

(5) Two closely related species are sympatric and tend to replace one another ecologically. Examples: *L. neoniger* and *L. crypticus, L. flavus* and *L. nearcticus.*

The effect of interspecific competition on variation. An interesting situation has been found in *Lasius* which may have an important bearing on the analysis of interspecific hybridization. This is the phenomenon of convergence of related species under the condition of reduced competition to give the false appearance of introgressive hybridization. *Lasius flavus,* for instance, can

be separated from *L. nearcticus* by at least eight genetically independent characters where these two species occur together in the eastern United States. In the western United States, where *nearcticus* is rare or absent, *flavus* converges toward it morphologically and assumes as part of an increased variability all but two of the diagnostic *nearcticus* characters. Furthermore, the characters occur together in a variety of combinations. (See under the section on geographic variation in *flavus*.)

A similar but less striking case occurs in *L. niger*. In those parts of North America and eastern Asia where its sister species *alienus* is uncommon, *niger* converges toward and partly overlaps *alienus* in quantity of standing appendage pilosity, the principal character separating the two species. In Europe, where both species are abundant, the two stand far apart in this character, with no sign of overlap. (See under the section on geographic variation in *niger*.)

The importance of this phenomenon is that it illustrates the pronounced effect interspecific competition can have on geographic variation. It also raises a serious objection to the method proposed by Anderson (1951) of using "concordant" versus "discordant" variation in the detection and evaluation of interspecific hybridization. According to Anderson, the occurrence of discordant (poorly correlated) character variation in a population of plants can be taken as an indication of introgression of genes from a related species. In *Lasius flavus* just the reverse of the condition described by Anderson for plants exists. Where *nearcticus* is in contact with it, *flavus* shows discrete, concordant variation. Where *nearcticus* is absent, the variation is discordant and convergent toward *nearcticus*. Whether a similar condition can exist in plant species remains to be seen, but it remains an important alternative explanation which must be taken into account in future hybridization analyses.

THE SPECIES AND SUBSPECIES CONCEPTS

The treatment of these lesser categories is crucial in a genus with a complex nomenclature such as *Lasius*. My own general views on the subject have already been expressed in a recent paper by W. L. Brown and myself (Wilson and Brown, 1953). We consider that the species represents the only taxonomic unit

approaching reality in nature. We agree with E. Mayr (1949a) that the species is only completely objective in terms of local faunas, i.e. where discrete populations co-exist at the same place at the same time. There is a sound evolutionary principle underlying this conclusion. When first brought together in nature any related populations that possess imperfect intrinsic isolating mechanisms will tend to take one or the other of two courses: either they will dispose of all imperfect reproductive barriers that may have arisen during their previous geographic isolation, and completely intergrade to become a single species; or else they will strengthen the reproductive barriers until hybridization is eliminated and thus insure permanent segregation. It is to be expected that intermediate degrees of reproductive isolation would be rare, since interspecific hybrids tend to be sterile and otherwise selectively disadvantageous and therefore an unprofitable venture for the contributing parental populations. There has been some genetic documentation of this crucial step in speciation (see Dobzhansky, 1952, p. 208), and it is borne out as a taxonomic fact that within or between sympatric populations hybridization is in almost every case either complete or else totally absent.

Of course, no such selective force can operate on geographically isolated populations, and it is probable that under this condition every stage of potential reproductive isolation can and does occur with equal frequency. The status of such populations — whether they are conspecific or distinct — can be judged only arbitrarily by comparing their degree of morphological divergence with that existing between sympatric populations of known status.

We have argued, and still argue, that the subspecies, or geographic race, cannot achieve the reality of the sympatric species and must of necessity be arbitrarily defined if it is to be recognized as a category at all. There are several reasons for this, chief among which is the tendency for genetically independent characters to show discordant geographic variation. As a consequence of discordance, the precise limits of any subspecies are set by the character or character combinations chosen by the describer. There is no such thing as a ''natural'' subspecies which can be handily delimited by whatever characters happen to be taxonomically convenient. It is our view that geographic

variation should be described in terms of each independent character, and not in terms of geographic segments designated by trinomens. A subspecies pattern fitted with trinomens may be satisfactory so long as only the characters originally employed to describe the pattern are used, but it becomes untenable, and the trinomens artificial and cumbersome, as variation in other characters is studied in more detail.

We have often heard the counterargument that it is the job of the taxonomist to describe variation as completely as possible, and that the designation of trinomens is a desirable part of this process, even if further analysis will eventually necessitate their rearrangement or total dissolution. But what function does the trinomen really perform once it is installed? To answer this question we must first consider the more elementary one, what function does labelling of any sort perform? Few will disagree with the answer that above all things it provides a system of reference for collateral studies in other fields of biology. The mere cataloging of individual specimens will contribute very little to science until it has found application in these studies. It would seem to follow that when a trinomen is used in a study other than a purely taxonomic one, all of its theoretical difficulties will likely become practical deadfalls. In the matter of discordant variation, the physiologist may go astray by expecting variation patterns in physiological characters to show a resemblance to those in the diagnostic morphological characters used by the taxonomist. The ecologist will often encounter variation in habitat preference or food habits which is not indicated by morphological subspecies patterns or which may even run counter to them. The student of speciation may be satisfied to analyze evolution in terms of subspecies units, but he will never accomplish more than a crude description of the process as long as he regards his units as being basic and objective.

Beyond the realm of purely descriptive, ornamental taxonomy, the trinomen is at its worst misleading and at its best superfluous. It may seem at first a convenient kind of shorthand in describing infraspecific variation, but it is far inferior to the direct analysis of genetically independent characters (and subsequent synthesis) with the goal of establishing extent and significance of concordance. With this conclusion as a guiding philosophy I have proceeded in the present revision to synonymize all trino-

mens, even where they might otherwise have been applied to taxonomically recognizable geographic segments, or "subspecies" in the conventional sense. I cannot see that the classification of *Lasius* will suffer in any way from this move; in fact, the limitation of scientific names to the binomen as undertaken here seems to produce the most lucid and practical classification possible within the confines of our present knowledge.

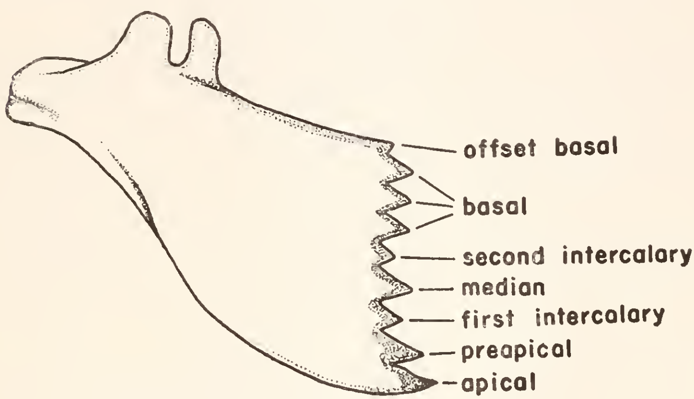
TERMINOLOGY AND MEASUREMENTS

Terminology in the descriptive part of this study follows, as closely as possible, usage prevalent in recent myrmecological literature. To fit the peculiarities of the genus, a few special measurements and indices have been devised. These are presented, along with a few possibly equivocal terms which need precise definition, in the glossary below. All measurements were made with an ocular micrometer fitted in a binocular dissecting microscope at a magnification of 37×. The micrometer span of 100 units covered a distance of exactly 2.97 mm.; measurements made with it were converted to millimeters by means of equivalent ratios. Most measurements were made to the nearest two-tenths of a unit, giving a calculated maximum error of ± 0.006 mm. Duplicate test measurements of pronotal width, head width, and scape length on the same specimens at an interval of several months concurred precisely in the majority of cases, differed by 0.2 unit in less than one-third of the cases, and hardly ever differed by as much as 0.4 unit. It is therefore safe to say that the measurements of these three most important dimensions have been very consistent in the course of the study, insuring accurate ratios and indices, and that they are probably precise to within a margin of ± 0.01 mm. or less. Other, grosser measurements, such as the head width and thorax width of the queen, probably have a somewhat larger margin, but in no case does it exceed ± 1 unit, or ± 0.03 mm.

Alitrunk. The entire median tagma of the body, consisting of the fused true thorax and propodeum.

Allometry. A size relationship betwen two structures or between a structure and the entire body, such that a dimension of one is a simple power function of a dimension of the other. In the present study the term is used in its more limited sense,

implying disproportionate growth between two organs. An understanding and use of the concept of allometry is essential in the taxonomy of a genus such as *Lasius,* where absolute measurements or indices are of little value unless expressed as a function of total size. The conventional method of representing allometry is by means of a double logarithmic graph, which con-



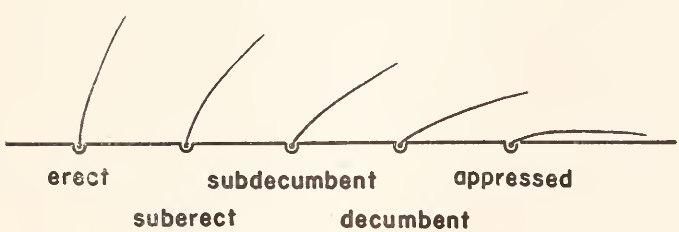


Fig. 3. *Above,* mandible of *L. sitkaensis,* showing the generalized formicine dentition and attendant nomenclature used in the present study. The offset basal tooth is a primitive character in the genus. *Below,* the nomenclature used in the present study to describe inclination of pilosity with respect to the cuticular surface.

verts the exponential curve into a straight line. However, size variation in *Lasius* is not sufficiently great to allow the expression of a curvilinear form and so all the graphs represented herein are simple arithmetical ones. Data are plotted individually in scatter diagrams, and the patterns they form are termed "regression zones."

Allopatric. Applied to populations occupying mutually exclusive ranges during the breeding season.

Cephalic index (CI). Head width $\times$ 100/head length.

Cryptic species. A species which so closely resembles other species that it is difficult or impossible to detect by the use of conventional taxonomic characters.

Dentition. A survey of the Formicinae made in connection with this revision has revealed the presence of a widespread elementary pattern in mandibular dentition. This pattern, exemplified by *Lasius,* has been provided with a special terminology illustrated in Figure 3. An offset basal tooth is a primitive character in *Lasius* and is present in only a few species of the genus.

Eye length (EL). The maximum measurable length of the eye.

Eye width (EW). The maximum width of the eye measured at a right angle to the long axis.

Head length (HL). The length of the head, held in perfect full face, measured from the midpoint of the anterior border of the median clypeal lobe to the midpoint of the occipital border.

Head width (HW). Worker and queen: the maximum width of the head held in perfect full face and excluding the eyes. If the eyes extend beyond the lateral borders of the head in this position, the measurement is taken across whatever part of the lateral borders are left exposed. *Male:* the maximum width of the head across and including the eyes.

Maxillary palpal length (ML). The maximum length of the terminal segment of the maxillary palp, measured from the distalmost part of the rim of the penultimate segment to the tip of the terminal segment.

Nidotype. A specimen from the same nest as the holotype or lectotype.

Paramere length. The length as defined by Clausen (1938), measured exactly parallel to the long axis from the level of the distalmost part of the basiparamere to the level of the tip of

the paramere.

Perfect full face. The head as seen in frontal view when held so as to attain maximum length and with the anterior border of the median clypeal lobe and occipital border horizontally aligned.

Pilosity. The longer, stouter hairs, or setae, which are outstanding above the shorter, usually finer hairs which constitute the pubescence. A special terminology, adopted from an unpublished doctoral thesis by F. G. Werner (Harvard University, 1950) and illustrated in Figure 3, has been employed herein to describe the angle of inclination from the cuticular surface.

Pronotal width (PW). The maximum width of the pronotum measured from directly above and at a right angle to the long axis of the alitrunk.

Propodeum. The equivalent of the "epinotum" of most earlier myrmecological work, i.e. the first segment of the abdomen which is, in higher Hymenoptera, fused to the thorax to form with it a single structure, the alitrunk.

Pubescence. The shorter, usually finer hairs underlying the pilosity (see definition above). The terminology of Figure 3 relating to angle of inclination applies to pubescence as well as to pilosity.

Scape index (SI). Scape length $\times$ 100/head width.

Scape length (SL). The maximum measurable length of the scape exclusive of the basalmost "neck".

Seta count. The number of standing hairs (see definition below) which can be seen extending beyond the outline of the following appendage surfaces: the anterior scape surface viewed in line with the plane of funicular flexion, and the outer surface of the fore tibia viewed in line with the plane of tibial flexion.

Standing hair. A hair which is subdecumbent, suberect, or erect, i.e., forming an angle with the cuticular surface of 45° or more.

Subgenital plate. In the male, the terminal sternite (IX) just underlying the genitalia.

Sympatric. Applied to populations the breeding ranges of which overlap, at least in part.

Key to the Species of Lasius, Based Principally on the Workers: Nearctic

1. Maximum worker eye length 0.20 × the head width or more.........2
   Maximum worker eye length 0.17 × the head width or less..........7

2. In a given nest series all larger *workers* (PW 0.57 mm. or more) and most smaller workers with one or more offset teeth at the basal angle of the mandible; *male* mandible with a narrow preapical cleft setting off a narrow, acute apical tooth, and with a well defined basal angle (Pl. 1) ....*sitkaensis* Pergande
   Workers of all sizes with the posterior basal tooth aligned with the adjacent teeth of the masticatory border; *male* mandible lacking a narrow preapical cleft and well-defined basal angle, the masticatory border curving gradually into the basal border (Pl. 1) 3

3. Maximum eye length usually less than 0.25 × the head width and never more; color always yellowish brown; scapes always lacking standing hairs (southwestern U. S. and Mexico) ....*sitiens* Wilson
   Maximum eye length exceeding 0.25 × the head width, even if only slightly; color occasionally yellowish brown, but then the scapes have standing hairs 4

4. In one or both mandibles of a majority of the nest series, either the penultimate basal tooth is markedly reduced in size relative to the two flanking teeth, or the gap between the penultimate and terminal basal teeth tends to be larger in area than the terminal basal tooth and variable in shape; when viewed with the mandibles opened and the head held in perfect full face (at maximum head length and with the occipital and anterior clypeal borders horizontally aligned), the anterior border of the median clypeal lobe is angulate, i.e. formed of two straight sides meeting at the midline to form an obtuse, usually pointed angle (Pl. 1) 5
   In all of the workers of a nest series, with rare exceptions, the penultimate and terminal basal teeth are subequal in size, and the gap between them has about the same area as the terminal tooth and is constant in shape; when viewed with the mandibles opened and the head held in perfect full face, the anterior border of the median clypeal lobe describes an even, broad parabolic curve, with the sides at least feebly convex and only occasionally meeting in a point at the midline (Pl. 1) 6

5. The scapes and tibiae of all workers except nanitics (PW less than 0.40 mm.) bearing standing hairs; body color light brown to medium brown, very rarely dark brown ....*neoniger* Emery
   The scapes and tibiae lacking standing hairs and usually without hairs

of any inclination (but pubescence still abundant); color typically dark brown .... *crypticus* Wilson

6. Within the size range PW 0.53–0.70 mm., scapes and tibiae bearing few or no standing hairs, the seta count (see under Terminology and Measurements) always less than 20 and usually less than 10 (refer to the PW-seta count regression zones of Fig. 6) .... *alienus* (Foerster)
   Within the above size range, the scapes and tibiae bearing numerous standing hairs, the seta count usually greater than 10 (western U. S. only) .... *niger* (Linnaeus)
7. Dorsal crest of the worker petiole seen in frontal view strongly convex and non-emarginate .... *humilis* Wheeler
   Dorsal crest of the worker petiole at most feebly convex and often emarginate 8
8. Eyes with less than 35 ommatidia 9
   Eyes with 35 or more ommatidia 11
9. Outer surfaces of each tibia with numerous standing hairs prominent above the ground pubescence (western U. S.) .... *fallax* Wilson
   Outer surfaces of each tibia with at most one or two standing hairs..10
10. Terminal segment of the maxillary palp longer than the penultimate segment in at least a majority of the workers of the nest series (eastern North America to Wyoming) .... *nearcticus* Wheeler
   Terminal segment of the maxillary palp in all of the workers of the nest series at most as long as the penultimate segment (Nova Scotia to California) .... *flavus* (Fabricius)
11. At least a broad longitudinal median strip of the second gastric tergite, exclusive of the extreme posterior portion, almost completely devoid of pubescence of any kind and with only a few widely scattered standing hairs, its cuticular surface extremely smooth and shining at low magnifications (eastern U. S.) .... *speculiventris* Emery
   Central area of second gastric tergite covered by abundant pubescence and standing hairs, its surface feebly shining to subopaque at low magnifications 12
12. Longest hairs of the posterior half of the first gastric tergite, exclusive of the extreme posterior strip, not exceeding in length 0.50 $\times$ the maximum width of the hind tibia at its midlength.................
   .... *umbratus* (Nylander)
   Longest hairs of the posterior half of the first gastric tergite, exclusive of the extreme posterior strip, at least 0.60 $\times$ as long as the maximum width of the hind tibia at its midlength 13
13. *Worker:* body color brownish yellow; lateral tibial surfaces completely lacking standing hairs; longest hairs of the posterior half of the first gastric tergite, exclusive of the extreme posterior strip, often as long as the maximum width of the hind tibia at midlength or longer;

pubescence of gastric tergites dense, often lending a greyish overcast to the cuticle under low magnifications; *queen* small, HW 1.02–1.17 mm. (eastern North America) .... *minutus* Emery

Worker: body color clear yellow; lateral tibial surfaces often with standing hairs; longest hairs of the posterior half of the first gastric tergite, exclusive of the extreme posterior strip, never exceeding 0.80 × the maximum width of the hind tibia at midlength; pubescence of gastric tergites lighter, rarely dense enough to lend a greyish overcast to the cuticle; *queen* larger, HW never less than 1.30 mm. 14

14. Pilosity of posterior half of first gastric tergite, exclusive of the extreme posterior strip, at least in part decumbent-subdecumbent; standing hairs sparse or absent on the lateral tibial surfaces (maritime Canada to Arizona) .... *subumbratus* Viereck

Pilosity of posterior half of first gastric tergite, exclusive of the extreme posterior strip, almost entirely suberect-erect; standing hairs often abundant on the lateral tibial surfaces (Pacific Coast to Idaho) .... *vestitus* Wheeler

Key to the Species of Lasius, Based Principally on the Workers: Palaearctic[1]

1. Maximum worker eye length 0.20 × the head width or more 2

Maximum worker eye length 0.17 × the head width or less 6

2. In *workers* with HW 0.79–1.21 mm., the SI ranges 82–94 and is usually 91 or less (see Fig. 5); alitrunk and petiole homogeneous light reddish brown, contrasting against the dark brown gaster; scapes and tibiae lacking standing hairs and usually hairs of any inclination; body pilosity sparse, the curving portion of the occipital corners viewed in full face typically devoid of hairs, rarely with one or two; *males* large, HW 1.04–1.10 mm. in three nest series examined; mandible with a shallow cleft separating the anterior and posterior halves of the masticatory border .... *brunneus* (Latreille)

In *workers* with HW 0.79–1.21 mm., the SI is 95 or more; body coloration variable, rarely exactly as in *brunneus;* scapes and tibiae often with standing hairs; curving portion of occipital corners usually with two or more standing hairs; *males* with HW rarely greater than 1.04 mm., usually less than 1.00 mm.; mandible lacking a clearcut cleft on the masticatory border 3

3. In workers with HW 0.86–1.12 mm., the SI ranges 112–124; if outside this HW range, then the SI should fit an extrapolation of the SI-HW regression zone shown in Figure 5 (Japan) .... *productus* Wilson

Within the same worker HW range, SI does not exceed 109 and is usually

[1] Excludes *L. buccatus* Stärcke and *L. teranishii* Wheeler, members of the subgenus *Dendrolasius* known only from sexual forms; see key to the queens.

much less 4

4. The worker possessing at least one and usually both of the two following characters: (1) alitrunk and petiole yellowish red, contrasting with the medium to dark reddish brown head and gaster (body tending to concolorous reddish brown in the Balkans area; see under geographic variation of this species); (2) scape with numerous preponderantly subdecumbent hairs. In addition, SI is 103–109 within a HW range of 0.61–1.10 mm. (Europe) ....*emarginatus* (Olivier)

   Worker body concolorous reddish brown to blackish brown; within the range of *emarginatus* in Europe, the scape either lacks standing hairs or these are preponderantly suberect-erect. In all populations of *alienus* except that in the Balkans area, and in all of *niger* except those in North Africa, the Balearics, the Atlantic Islands, and eastern Asia, the SI is 95–103 within a HW range of 0.61–1.10 mm. 5

5. In workers with PW 0.53–0.70 mm., scapes and tibiae with few or no standing hairs, the seta count (see under Terminology and Measurements) always less than 20 and usually less than 10. *alienus* (Foerster)

   Within the above size range, European workers usually possess seta counts of 20 or more; Asiatic workers often range below this and in some cases may be distinguishable only by comparing intranidal trends with the regression zones of Figure 6......*niger* (Linnaeus)

6. *Worker* body color jet black; the scutum of the *queen* seen in perfect side view overhangs the pronotum and claims the entire anterior thoracic convexity 7

   Worker body color yellow to yellowish brown; the scutum of the queen does not overhang the pronotum but shares with it the anterior thoracic convexity 9

7. Antennal scapes of the worker flattened to the extent that for most of their length the minimum measureable width at any point is less than half the maximum measurable width at that point; the *queen* is an extreme ''beta'' form, with greatly flattened scapes, femora, tibiae, and metatarsi (Japan and Korea) ....*spathepus* Wheeler

   Antennal scapes of the worker short-elliptical in cross-section, so that for most of their length the minimum width at any point is 0.8 × the maximum width at that point or more; the *queen* is an ''alpha'' form, with normal appendages, the scape short-elliptical in cross-section 8

8. *Queen* with many body and appendage hairs curved at the tip or sinuate, those on the appendages often curving back to touch the cuticular surface again; body pubescence sparse or absent, the cuticular surface smooth and shining; *worker* (tentatively associated) with the standing hairs of the second and third gastric tergites (exclusive of

the extreme posterior strips) reaching a maximum length of 0.10–0.12 mm. and as long as the standing hairs on the pronotum or longer; in side view the petiolar crest thin and sharp (Pl. 2, fig. 8) (Japan and Korea) ....*crispus* Wilson

Queen with few or no hairs curved at the tip or sinuate; body covered with abundant appressed pubescence which at least partly obscures the shining cuticular surface; *worker* with the standing hairs of the second and third gastric segments (exclusive of the extreme posterior strips) never as long as 0.10 mm. and rarely exceeding 0.08 mm., usually shorter than the standing hairs of the pronotum; the petiolar crest in side view thicker and blunter (Pl. 2, fig. 7) (England to Japan) ....*fuliginosus* (Latreille)

9. Dorsal crest of the worker petiole seen in frontal view strongly convex and never emarginate 10

Dorsal crest of the worker petiole at the most feebly convex and often emarginate 11

10. Eyes of *worker* set in shallow but distinct circumocular depressions; pilosity of first gastric tergite predominantly decumbent; PW not exceeding 0.63 mm.; *queen* exceedingly small, HW 0.76–0.78 mm..... ....*carniolicus* Mayr

Eyes of *worker* not set in depressions; pilosity of first gastric tergite predominantly subdecumbent-erect; PW of three workers measured 0.88–0.93 mm.; *queen* exceptionally large, HW of single specimen measured 1.99 mm. (known only from the Himalayas) ....*crinitus* (F. Smith)

11. Worker eyes with less than 30 ommatidia (if the nest series splits on this couplet, go to 12) 12

Worker eyes with more than 30 ommatidia 13

12. Scapes and tibiae of worker with numerous standing hairs prominent above the ground pubescence (eastern Asia) ....*talpa* Wilson

Worker scapes and tibiae with few or no standing hairs (England to Japan) ....*flavus* (Fabricius) in part

13. In both the worker and queen, the dorsal border of the petiole in frontal view narrow and deeply emarginate, the depth of the emargination measured from the level of the bicornuate dorsal crest to the bottom of the emargination at least as great as the width of the emargination measured at the level of the middle of the depth measurement ....*bicornis* (Foerster)

Dorsal border of the petiole with never more than a right-angular emargination 14

14. Either the genal margins of the *worker* seen in full face with standing hairs prominent above the ground pubescence; or else the longest hairs of the posterior half of the first gastric tergite (exclusive of

the extreme posterior strip) are distinctly less than half as long as the maximum width of the hind tibia at its midlength. In the *queen* the head width is about the same as the width of the thorax just anterior to the tegulae or greater ....
umbratus (Nylander) or *rabaudi* (Bondroit), (see key to queens).

Genal margins of *worker* seen in full face lacking standing hairs; the longest hairs of the posterior half of the first gastric tergite (exclusive of the extreme posterior strip) at least half as long as the maximum width of the hind tibia at its midlength. In the *queen* the head width is much less than the width of the thorax just anterior to the tegulae 15

15\. (A species known from only one nest series from the Himalayas.) Terminal maxillary palp segment of worker slightly longer than the penultimate segment; the segments as a whole longer (see under diagnosis of this species) ....*alienoflavus* Bingham

(A widespread and abundant Holarctic species.) Terminal maxillary palp segment of worker at most as long as the penultimate ....
..................................*flavus* (Fabricius), in part

Key to the Queens of Lasius[1]

1\. Metapleural gland opening provided with conspicuous guard hairs; in side view the scutum does not overhang the pronotum but shares with it the anterior thoracic convexity 2

Metapleural gland opening lacking guard hairs; in side view the scutum overhangs the pronotum and claims all of the anterior thoracic convexity 22

2\. HW distinctly less than the width of the thorax just anterior to the tegulae 3

HW about the same as or greater than the width of the thorax just anterior to the tegulae 13

3\. Length of terminal segment of maxillary palp exceeding 0.1 × the HW, even if only slightly 4

Length of terminal segment of maxillary palp less than 0.1 × the HW, even if by only a slight amount 10

4\. When viewed with mandibles opened and the head held in perfect full face (at maximum head length and with the occipital and anterior clypeal borders horizontally aligned), the median third of the anterior border of the median clypeal lobe is flat or emarginate; all the queens of a nest series with at least one and often two or three offset teeth present on the basal angle and along the basal border of the mandible (North America) ....*sitkaensis* Pergande

[1] Excluding the rare Himalayan species *alienoflavus* (see key to workers).

When viewed as above, the median third of the anterior border of the median clypeal lobe convex or angulate, never flat or emarginate; the posterior basal tooth, with rare exceptions, always aligned with the adjacent teeth of the masticatory border; when it is offset, this condition occurs in a minority of the individuals of the nest series and usually only on one mandible in any individual, and secondary offset teeth are never present on the basal border 5

5. When viewed with the mandibles opened and the head held in perfect full face, the anterior border of the median clypeal lobe is angulate, with two straight or very feebly convex sides meeting in a blunt point at the midline; in a large part of any nest series the penultimate basal tooth is distinctly reduced in size relative to the two flanking teeth (North American species only) 6

When viewed as above, the anterior border of the median clypeal lobe is broadly and evenly rounded; with rare exceptions the penultimate basal tooth is about the same size as the two flanking teeth 7

6. Scapes and tibiae with numerous standing hairs ....*neoniger* Emery

Scapes and tibiae lacking standing hairs ....
..........................*crypticus* Wilson and *sitiens* Wilson

7. Length of terminal segment of maxillary palp 0.32–0.34 mm. in the several series measured (Japan) ....*productus* Wilson

Length of terminal segment of maxillary palp not exceeding 0.26 mm...8

8. Scape with numerous standing hairs ....*niger* (Linnaeus)

Scape with few or no standing hairs, although decumbent hairs may be numerous 9

9. Scape with numerous decumbent hairs outstanding above the pubescence ....*emarginatus* (Olivier)

Scape with few or no decumbent hairs outstanding above the pubescence ....*alienus* (Foerster) and *brunneus* (Latreille)

10. Scape with numerous standing hairs (eastern Asia) ......*talpa* Wilson

Scape with few or no standing hairs 11

11. Tibiae with numerous standing hairs (western U.S.).....*fallax* Wilson

Tibiae with few or no standing hairs 12

12. Terminal segment of maxillary palp usually longer than the penultimate (see diagnosis) (eastern North America to Wyoming) ....
....*nearcticus* Wheeler

Terminal segment not exceeding in length the penultimate segment (Holarctic) ....*flavus* (Fabricius)

13. HW 0.76–0.78 mm.; petiole in side view thick, resembling an inverted U (Eurasia) ....*carniolicus* Mayr

HW exceeding 1.00 mm.; petiole in side view thinner, with a narrow dorsal crest 14

14. Alitrunk and gaster covered with extremely long, fine, predominantly appressed hairs; HW of single specimen measured 1.99 mm. (Himalayas) ....*crinitus* (F. Smith)
Pilosity of alitrunk and gaster otherwise; HW never exceeding 1.75 mm. 15

15. The dorsal border of the petiole in frontal view narrow and deeply emarginate, the depth of the emargination measured from the level of the bicornuate dorsal crest to the bottom of the emargination at least as great as the width of the emargination measured at the level of the middle of the depth measurement (Eurasia) .....*bicornis* (Foerster)
Dorsal border of the petiole with never more than a right-angular emargination 16

16. HW not exceeding 1.17 mm. 17
HW at least 1.40 mm. 18

17. First gastric tergite densely covered with coarse standing hairs, the longest of which exceed in length the maximum width of the hind tibia at its midlength (eastern North America) ....*minutus* Emery
First gastric tergite with relatively sparse, fine hairs, the longest of which do not exceed in length 0.8 × the maximum width of the hind tibia at its midlength (southwestern U. S.) ....*humilis* Wheeler

18. The longest hairs of the first gastric tergite exclusive of the extreme posterior strip not exceeding in length 0.5 × the maximum width of the hind tibia at its midlength 19
The longest hairs of the first gastric tergite, exclusive of the extreme posterior strip, about as long as the maximum width of the hind tibia at its midlength..21

19. Dorsal surfaces of second and third gastric tergites completely devoid of pubescence and strongly shining (eastern U.S.)..*speculiventris* Emery
Dorsal surfaces of second and third gastric tergites covered by appressed pubescence which often partly obscures the shining cuticular surface 20

20. Scapes conspicuously flattened, the minimum width at midlength not exceeding 0.10 mm. (Fig. 15) (Eurasia) ....*rabaudi* (Bondroit)
Scapes short-elliptical in cross-section, the minimum width at midlength not less than 0.11 mm. (Holarctic) ....*umbratus* (Nylander)

21. Pilosity of anterior gastric tergites predominantly erect.*vestitus* Wheeler
Pilosity of anterior gastric tergites predominantly decumbent-subdecumbent ....*subumbratus* Viereck

22. A "beta" form, with conspicuously flattened scapes, femora, tibiae, and metatarsi; thorax completely lacking hairs of any kind 23
An "alpha" form, showing no conspicuous flattening of the appendages; thorax with abundant hairs 24

23. Head about as broad as long; petiolar scale symmetrical in side view, with both the anterior and posterior faces gently convex ....*teranishii* Wheeler

Head much broader than long, anterior border of petiolar scale in side view angulate, being parallel with the posterior border up to the level of the petiolar spiracle but then bending abruptly back to form an oblique face up to the dorsal crest ....*spathepus* Wheeler

24. Many of the body and appendage hairs curved at the tip or sinuate, those on the appendages often curving back to touch the cuticular surface again; body pubescence sparse or absent, the cuticular surface smooth and shining ....*crispus* Wilson

Few or no hairs curved at the tip or sinuate; body covered with appressed pubescence which at least partly obscures the cuticular surface 25

25. A sharp median carina runs from the frontal triangle to a small shallow pit in the center of the clypeus; CI about 97 ......*buccatus* Stärcke

Median clypeal carina weakly developed and running most of the length of the clypeus, not ending in a central pit; CI as least 100 ....*fuliginosus* (Latreille)

Key to the Males of Lasius[1]

1. Metapleural gland opening provided with guard hairs 2

Metapleural gland opening lacking guard hairs 12

2. Mandible lacking a preapical cleft, at the most the masticatory border feebly impressed in the middle; basal angle of mandible always broadly rounded, the masticatory border curving gradually into the basal border 3

Mandible with a distinct preapical cleft (occasionally lacking in smaller individuals with HW less than about 1.00 mm.); basal angle often distinctly marked and clearly separating the masticatory and basal borders 6

3. SI exceeding 100 ....*productus* Wilson

SI less than 80 4

4. Standing hairs common on the scape ....*niger* (Linnaeus) and *neoniger* Emery

Standing hairs rare or absent on the scape 5

5. Subgenital plate arc-shaped, with a deeply concave posterior border sweeping back to the prominent posterolateral flanges, and with the anterior border correspondingly convex (Europe) ....*emarginatus* (Olivier)

Subgenital plate subquadrate, the posterior border flat or weakly con-

[1] The males of the following species are unknown or were not available during the present study: *alienoflavus, bicornis, crinitus, humilis, teranishii,* and *vestitus.*

cave and the posterolateral flanges weakly developed or absent ....*alienus* (Foerster), *crypticus* Wilson, and *sitiens* Wilson

6. HW exceeding 1.00 mm.; basal angle of the mandible indistinct, the masticatory border merging gradually into the basal border (Eurasia) ....*brunneus* (Latreille)
   Either HW less than 1.00 mm., or else the basal angle of the mandible is distinct and clearly demarcates the masticatory and basal borders...7
7. HW distinctly less than the width of the thorax just anterior to the tegulae 8
   HW at least as great as the width of the thorax just anterior to the tegulae (subg. *Chthonolasius*) 9
8. ML exceeding 0.10 mm. ....*sitkaensis* Pergande
   ML less than 0.08 mm. ....subg. *Cautolasius* (*flavus, nearcticus, talpa, fallax*)
9. At least a broad longitudinal median strip of the second gastric tergite completely devoid of pubescence, its cuticular surface shining (eastern U.S.) ....*speculiventris* Emery
   All of second gastric tergite covered with abundant pubescence which at least partly obscures the cuticular surface 10
10. Petiole in side view thick, with a broadly rounded dorsal crest; standing hairs abundant around the entire cephalic margin (seen in full face) posterior to the eyes (Eurasia) ....*carniolicus* Mayr
    Petiole in side view thin, with an acute dorsal crest; much of the cephalic margin posterior to the eyes bare of pilosity 11
11. Longest hairs of the first gastric tergite exceeding 1.5 × the maximum width of the hind tibia at midlength; longest hairs of the posterior two-thirds of the clypeus exceeding 0.16 × the HW (eastern North America) ....*minutus* Emery
    Longest hairs of the first gastric tergite not exceeding 1.1 × the maximum width of the hind tibia at midlength; longest hairs of the posterior two-thirds of the clypeus not exceeding 0.10 × the HW 12
12. Maximum length of the hairs of the first gastric tergite 0.9–1.1 × the maximum width of the hind tibia at its midlength (Nova Scotia to Arizona) ....*subumbratus* Viereck
    Maximum length of the hairs of the first gastric tergite not exceeding 0.7 × the maximum width of the hind tibia at its midlength ....*umbratus* (Nylander) and *rabaudi* (Bondroit)
13. Mandibles with seven well developed teeth including the apical; in frontal view the genae strongly convex, the head about as wide directly in front of the eyes as directly behind ......*buccatus* Stärcke
    Masticatory border of mandible smooth, or at most with several small, irregular denticulae; in frontal view the genae feebly convex, the head

directly in front of the eyes at the most 0.9 × as wide as directly behind the eyes 14

14. In side view the posterior margin of the petiolar scale is gently convex from the level of the posterior foramen to the dorsal crest, while the anterior border is parallel with it up to the petiolar spiracle and then turns abruptly posteriorly to produce a second face up to the crest (Japan and Korea) .... *spathepus* Wheeler

The petiolar scale in side view symmetrical, the posterior border showing the same degree of convexity as the anterior 15

15. The petiole in side view with a narrow, sharp crest (Japan and Korea) .... *crispus* Wilson

The petiole in profile with a thick, convex crest (England to Japan) .... *fuliginosus* (Latreille)

SYSTEMATIC TREATMENT BY SPECIES

Lasius sitkaensis Pergande
(Subg. *Lasius*)

Lasius niger sitkaensis Pergande, 1900, Proc. Wash. Acad. Sci., **2:** 519–520, worker; original description. Type locality; Sitka, Alaska.

Lasius niger var. *sitkaensis*, Wheeler, 1917, Proc. Amer. Acad. Arts Sci. Boston, **52:** 524, *part.*

Lasius niger neoniger, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 420, *part.* [*nec* Emery 1893].

DIAGNOSIS. *Worker* (1) All medium-sized and larger individuals (PW 0.57 mm. or greater) as well as many nanitics, with an "offset" tooth at the basal angle of the mandible, conspicuously smaller than the adjacent teeth of the masticatory border and often directed more posteriorly; this tooth may be succeeded posteriorly by one or (rarely) two serially arranged, smaller teeth on the basal border (Pl. I, Fig. 1). The entire basal angle, teeth included, tends to be rounded, not sharply angular as in the higher members of the subgenus.

(2) Subdecumbent to erect hairs common on scapes and fore tibiae of individuals with PW 0.57 mm. or greater. Size averaging larger than other members of the subgenus (see under further description below).

Queen. (1) Possessing an offset basal tooth similar to the worker's; secondary teeth on basal border very frequent.

(2) Clypeus lacking a perceptible carina; middle third of

the anterior border of the median lobe straight or shallowly concave.

(3) Scapes and fore tibiae with abundant subdecumbent to erect hairs.

Male. (1) Sclerotized setiferous area of the posterior margin of the subgenital plate (sternite IX) unilobed to bilobed, with all intermediate conditions, but never projecting beyond the unsclerotized rim, with the result that the entire posterior border within the lateral flanges is straight or nearly straight.

(2) Mandible with a well marked basal angle separating the masticatory and basal borders; a distinct apical tooth is set off by a deep, relatively narrow preapical cleft; the masticatory border is straight and frequently armed with irregular denticles which are best developed apicad and obsolescent basad, rarely extending past the midpoint of the border (Pl. 1, Fig. 4).

LECTOTYPE. By present selection, a worker in the MCZ labelled "Sitka, Alaska; June-99; T. Kincaid Coll. 80." PW 0.85 mm., HW 1.26 mm., HL 1.28 mm., SL 1.15 mm., SI 92, ML (right) 0.22 mm., EL 0.28 mm., seta count 40. Left mandible, viewed closed and *in situ,* with a single offset tooth at the basal angle; basal angle of right mandible not visible. Anterior border of median clypeal lobe broadly and evenly rounded, very slightly flattened medially; no carina visible. All of body and appendages light brown, appendages a shade lighter than body and approaching yellowish brown. Syntopotypes in MCZ, AMNH, and USNM.

FURTHER DESCRIPTION. *Worker.* In a sample of 266, with no more than 2 per nest series, PW range 0.40-0.89 mm., mean with standard error 0.650 $\pm$ 0.006 mm., standard deviation 0.084 mm. SI in 25 nest series measured (encompassing most of the size variation) formed an allometric regression zone intermediate between *brunneus* and *niger,* closer to *niger* but with the same slope as *brunneus* (*q.v.*), so that above PW of about 1.05 mm., *sitkaensis* diverged strongly from *niger* and showed little individual overlap with that species (see Fig. 5). Maxillary palp segments IV, V, and VI subequal; segment VI (ML) averaging about 1.03 $\times$ as long as the EW. The basal mandibular tooth very variable in nanitic workers; in series from incipient colo-

nies, where the worker PW averages 0.5 mm. or less, the mandibles vary from the "*niger* form", in which there is no offset basal tooth and the basal border runs straight to the edge of the first major tooth of the masticatory border, through a series in which the offset tooth appears as a variously developed convexity on the basal border, to the typical "*sitkaensis* form" already described. In incipient colonies, the majority of workers show some development of the offset basal tooth, while in larger colonies the frequency of the tooth approaches 100 per cent, and secondary teeth on the basal border are common. The masticatory teeth follow the general *Lasius* pattern well (Fig. 3), but the basal segment is more variable than in other members of the subgenus. There are typically three, and rarely four, basal teeth exclusive of and anterior to the offset tooth. Occasionally the second intercalary tooth is missing, or there is a secondary intercalary tooth developed between two of the basal teeth, or one of the basal teeth is bifurcate.

The clypeus appears evenly convex in full face and feebly emarginate when viewed antero-obliquely. Head and body broader and more massive relative to total length than in all other *Lasius s. s.* excepting *brunneus;* this difference is subject to allometric modification, since *sitkaensis* nanitics are little different in body form from medium-sized *niger* and *alienus,* while very large *niger* and *alienus* resemble closely, but not completely, medium-sized *sitkaensis.* Posterior margin of head concave in full face view. Promesonotal suture deeply impressed in medium-sized workers; this was a character proposed by Creighton (1950) to separate "*niger neoniger*" from "*alienus americanus*", but it can be used only with qualification, since it is strongly allometric and includes some interspecific overlap. Dorsal margin of petiole in frontal view flat to strongly convex, rarely emarginate.

Entire body, including occipital margin and gastric tergites, covered with abundant standing hairs. Standing hairs about as abundant on appendages as in *niger;* i.e. in the majority of nest series, workers with pronotal width around 0.24 mm. have seta counts between 20 and 40. A higher percentage of the hairs are subdecumbent than in *niger,* where nearly all are typically suberect-erect. The seta count is strongly allometric and is usually less than 10 in nanitics. Superimposed on the allometric variation

is a genetic one; the regression zone varies internidally. At one extreme (by nest series), nanitics with PW of 0.5 mm. or less give seta counts between 10 and 20, while workers with PW of 0.7 mm. or more often exceed 40. At the opposite extreme, nanitics give seta counts of 0 and larger workers usually fall below 20. Body pubescence well developed, tending to be denser on the genae and sparser on the gastric tergites than in *niger*, so that even to the naked eye the genae are notably more opaque and the gaster shinier than in that species.

Color usually overall light brown, but ranging from yellowish brown (rare) to dark brown (common).

Queen. HW 1.76-1.99 mm. Mandibular dentition varying as in the worker, except that the offset basal tooth is only rarely reduced to a mere convexity, and no example has been found in which it is entirely missing. In a majority of cases the anterior border of the median clypeal lobe (seen in perfect full face) is emarginate to some degree; it is never convex as in other *Lasius*. The head is more massive relative to the thorax and the occipital zone is broader relative to the anterior part of the head than in other members of the subgenus, but this is probably in part a simple function of the larger total size attained. Standing pilosity with same density as in the worker, showing similar allometric and genetic variation. Hairs of scape shorter and finer than in *L. niger*, the standing hairs seen dorsally and perpendicular to the plane of articulation seldom longer than one-third the greatest width of the scape. Color and pubescence as in the worker. Wings overall infuscate, rather faintly in the distal two-thirds and darkest in the costal cell and area proximal to the discoidal cell.

Male. HW 0.81-0.95 mm. Mandible never differing substantially from the main diagnostic features previously stated, i.e. always possessing a sharp preapical cleft and a well defined basal angle. The masticatory denticles, on the other hand, are highly variable. Usually two denticles are present, but there may be three or none, and they are always irregular in size and placement. In one exceptional series (Rico, Dolores Co., Colo.; MCZ) denticles were developed on the basal angle.

Clypeus lacking a median carina, the anterior border of its median lobe broadly rounded. Dorsal margin of the petiole variably convex, occasionally flat or feebly emarginate.

That part of the posterior margin of the subgenital plate inclosed in the posterolateral flanges always straight to feebly convex in the many specimens dissected; the sclerotized posterior setiferous lobes do not push out beyond the transparent posterior margin of the plate to form a conspicuous convexity as in many other members of the subgenus. The degree of lobing within the setiferous area varies greatly within single nest series. One nest series studied (Morris, Ramsey Co., N. Dak.; P. B. Kannowski leg.; G. C. Wheeler Coll.) exhibited almost all of the maximum variation for the species, the posterior setiferous margin ranging from straight to bilobed. Another series from the same locality showed the alternative condition, a single median lobe. Paramere broadly finger-shaped, typically narrower than in related species, its width at midlength about ⅕ to 1/3 its length. Paramere length relative to head width similar to the European population of *L. niger* (Fig. 7); HW/paramere length ratios measured in 16 nest series varied between 0.95/0.33 and 0.82/0.37 (in mm.); absolute paramere length ranged 0.28-0.37 mm. Volsella typical for genus. Pygostyle broadly finger-shaped, the tip about as wide as the membranous base.

Appendages with dense pubescence but with standing hairs much sparser than in worker and predominantly subdecumbent-suberect. Seta count seldom if ever exceeding 10, usually 5 or less, and often 0. Body hairs notably sparser than in the worker and queen, but still abundant over the alitrunk and entire surfaces of the gastric tergites. Body color medium brown to black, the appendages light to dark brown; both overall lighter than in other members of the subgenus. In lighter specimens the head is typically darker than the alitrunk and the alitrunk darker than the gaster and appendages.

GEOGRAPHIC VARIATION. *Sitkaensis* is surprisingly uniform over its entire range, despite the occasional occurrence of striking variation within single nest series or local populations. A single weak unilateral trend is found in the northwestern segment of the range, including British Columbia and Alaska. In this area there have been encountered a significantly higher percentage of series with sparse appendage pilosity. Partly correlated with this character is a darkening of color. Unfortunately both characters are highly subjective, and intermediate conditions are very difficult to judge. I have attempted to cope

with this situation by placing each series in one or the other of two classes for each character: extreme depilation (PW 0.5 mm. with seta count 0, PW 0.8 mm. with seta count less than 20) is marked *h* and dark brown coloration is marked *l*, while the opposing extreme conditions and intermediate conditions are marked together as *H* and *L*. A crude picture of the geographical trend can be drawn by listing and classifying the series studied from that segment of the range bounded by Alaska, Washington, Alberta, and western Montana. ALASKA: Sitka (LH); Ketchikan (lh, 2 series; Lh, 1 series); Metlakatla (Lh); Forrester Is. (Lh, 2 series, LH, 1 series); Wrangell (lh, 2 series); Port Beauclerc, Kuiu Is. (Lh); Point Barrie, Kupreanof Is. (lh). BRITISH COLUMBIA: Penticton (LH); Terrace (LH, 1 series; Lh, 1 series); Victoria Chase (LH); Keremeos (LH); Glacier (lh); Chilliwack Valley (lh); Howser, Selkirk Mts. (LH); Royal Oak, Vancouver Is. (LH); Alert Bay, Vancouver Is. (lH). ALBERTA: Red Deer (LH); Macleod (LH). WASHINGTON: Pullman (LH); Seattle (LH); Bay Center (Lh); Three Brothers Mt., Olympic Range (lH); Tacoma (LH); Metaline Falls, Pend Oreille Co. (LH); Milan, Spokane Co. (LH). IDAHO: Troy, Latah Co. (LH); south slope of Moscow Mt., Latah Co. (over 100 colonies examined in the field, nearly all LH, see below); Hyndman Creek, Challis Nat. For., Blaine Co. (lh). MONTANA (western half): St. Mary, Glacier Co. (lh); Flathead Lake (LH); Phillipsburg, Granite Co. (Lh); Troy, Lincoln Co. (LH); Sula, Ravalli Co. (LH).

Beyond this area, to the south and east, the two extreme characters *l* and *h* become much rarer, constituting less than 5 per cent of the total population. Following are the exceptional records in which they do occur. OREGON: Anthony Lake, Blue Mts., near Pendleton, 7000 feet (lh). CALIFORNIA: Lake Tahoe (Lh). WYOMING: Isa Lake, Yellowstone Nat. Pk., 8300 feet (Lh, 2 series). NEW MEXICO: Hyde State Park, Santa Fe Co., 8600 feet (Lh, 2 series); Ute Park, Colfax Co., 7400 feet (lH, 1 series; LH, 1 series); 15 miles north of Eagle Nest, Colfax Co., 9500 feet (lh).

It appears that *l* and *h* occur at least partly independent of one another, that they are most frequent in the extreme Northwest, and that they diminish southward and eastward. Beyond these limited data, there is some evidence to suggest that *l* at

least may be environmental in origin. In six out of the seven records for *l* cited from south of Washington and Montana, the colonies were found at what probably represents the upper elevational limit for *sitkaensis* in each area. The Isa Lake series, for example, were taken by myself in spruce-fir woods at 8300 feet on the south slope of Craig Pass, well above the next highest record for the genus in Yellowstone Park (6800 feet). Both colonies were small, composed of nanitic workers, and situated under rocks in clearings in the forest; they were the only *Lasius* found in the vicinity and gave every impression of living under conditions of marginal existence. An incipient colony of similar type was taken at 5300 feet on Moscow Mountain, Idaho, well above the bulk of the dense *sitkaensis* population resident on this mountain. The workers of this colony were much darker than those taken from colonies at lower elevations, including another incipient colony found at 3500 feet. In the light of this evidence I consider that the extreme dark coloration (*l*) may be due partly or wholly to some environmental feature of high elevation such as lower temperature. There may be in effect a high elevation ecophenotype characterized by depauperate colonies of dark, nanitic workers and comprising a regular feature of populations in mountainous areas.

DISTRIBUTION. *L. sitkaensis* has the northernmost distribution of all the Nearctic members of the genus (Fig. 4). It occurs from eastern Quebec to southeastern Alaska, south in the East to Massachusetts, with an isolated population in the southern Appalachians of North Carolina, and south in the West to the San Jacinto Mountains of southern California and the higher isolated ranges of southern Arizona.

The extreme northeastern record is the mouth of the Matamek River, Quebec, on the north coast of the Gulf of St. Lawrence (H. Eidmann leg.; USNM). I have seen numerous series from throughout the maritime provinces of Canada, including New Brunswick, Nova Scotia (with Cape Breton Island), and Prince Edward Island. The species ranges over Maine, reaching the extreme southeast of the state at Saco and Kittery Point (MCZ); a random collection of *Lasius* made at the former locality for me by W. L. Nutting indicates that *sitkaensis* is far outnumbered there by *L. neoniger*. A single collection of winged reproductives in flight has been made at Marblehead, Mass. (G. C. Wheeler leg.

and Coll.), but the species must be rare this far south, because I have never collected it myself in the course of many field trips in eastern Massachusetts. It occurs in New Hampshire (Mt. Washington summit, male; C. S. Bacon leg., MCZ; Bowman and Bretton Woods, White Mts., E. O. Wilson and W. L. Brown leg., MCZ; lower east slope of Mt. Monadnock, W. L. Brown leg.,

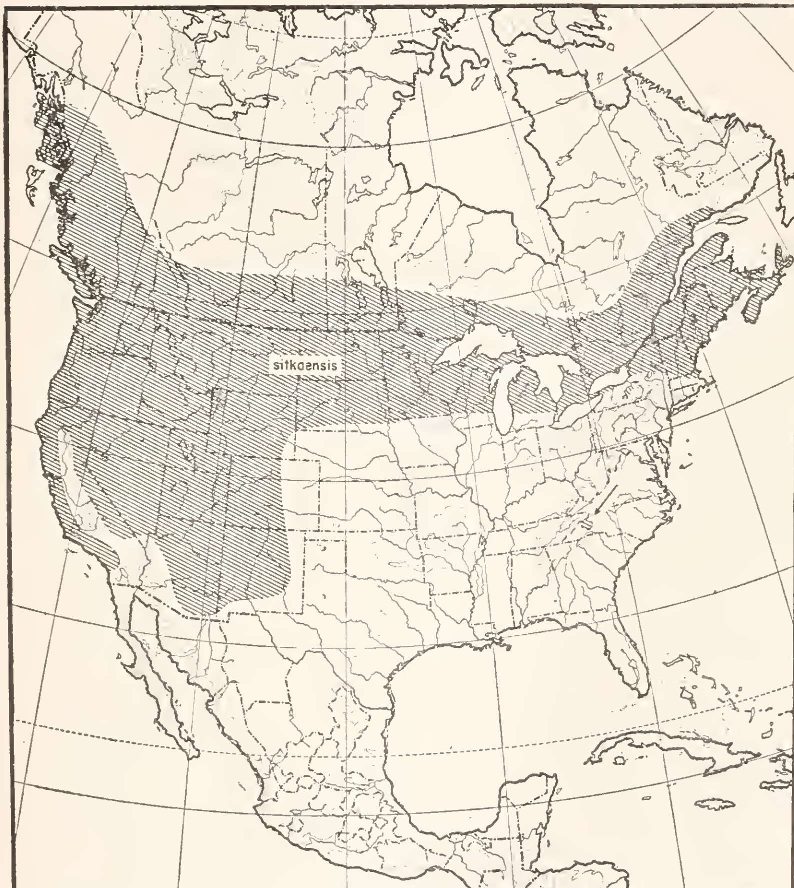


Fig. 4. An outline of the known distribution of *L. sitkaensis.* (This and subsequent outline maps used with permission of the University of Chicago Press.)

MCZ) and Vermont (Proctor Piper State Forest; W. S. Creighton leg. and Coll.). I found a single colony in the midst of a dense *neoniger* population at Plattsburg, upper New York, and I have seen specimens from Lanesville, Catskill State Park, in the same state (K. Christiansen leg.; MCZ).

The southern Appalachian population represents a remarkable case of discontinuous distribution. Several colonies were found by A. C. Cole, A. Van Pelt, and myself in the summer of 1951 along the Blue Ridge Parkway northeast of Ashville, North Carolina, in the vicinity of Mt. Mitchell and nearby Craggy Gardens. These were all under rocks at the edge of spruce-fir and beech forests at elevations between 5000 and 5200 feet. This elevation range happens to include the upper limit for *L. neoniger* in the area, although this species still vastly outnumbers *sitkaensis* there. *Neoniger* shows a predilection for open situations and is the dominant ant along the grassy roadstrips. *L. alienus* occurs sporadically in rotting wood at the forest border. That the *sitkaensis* at this locality really belong to a restricted and completely isolated population is supported by considerable evidence. The northeast population obviously thins out in a southward direction in New England. I have never encountered it among the thousands of series of *Lasius* I have examined from the intervening area. It was not found in the exhaustive collection of ants made by Cole in the Smoky Mountains of Tennessee, and neither Cole, Van Pelt, nor have I ever taken it in the course of many field trips in the adjacent lowland areas of North Carolina and Tennessee. It remains to be seen whether other populations occur under isolated circumstances and at suitable elevations elsewhere along the course of the Appalachians.

West of New England, *sitkaensis* has been taken at several localities in Michigan and probably occurs over most of the state. I found a single colony in sand dune country near Marquette, on the northern peninsula, again inclosed in a dense population of *neoniger;* several other collections made by others in the same area suggest that it is a common species there. The southernmost record for the state is the Edward S. George Reserve, Livingston Co. (M. Talbot leg. and Coll.). Dr. Talbot's collections, made in conjunction with her recent intensive study of the ant fauna of the Reserve, have revealed *sitkaensis* to be an uncommon

species there, greatly outnumbered by both *neoniger* and *alienus*.

Sitkaensis probably occurs over all of Minnesota; it was abundantly represented in a large collection of the genus made by Kenneth Kraft in Itasca State Park. I have seen a single series from Dickinson Co., Iowa, but the species must be rare this far south, since it was not present in a substantial collection made by R. L. King in several areas of Iowa, including Dickinson County. The species is apparently abundant over all of North Dakota, as indicated by the multitude of collections made over the past twenty-five years by G. C. Wheeler and his students. It has been taken on two occasions at Hill City, South Dakota (T. Ulke leg., MCZ; Creighton leg. and Coll.).

The records from Alaska to Washington and eastern Montana have been listed in the previous section on geographic variation. In the western United States *sitkaensis* is abundant along the entire length of the Rockies and Cascade-Sierras. It has been taken as far south as the Tanquitz Valley of the San Jacinto Mts., Calif. (USNM); Ramsey Canyon, Huachuca Mts., Ariz.; Rustler Park, Chiricahua Mts., Ariz.; and Hospital Flat, Graham Mt., Ariz. (the last three W. S. Creighton leg. and Coll.). It also occurs on isolated forested mountains through the Great Basin. Judging from many collections mostly by A. W. Grundmann (in Cole Coll.) it is abundant on the mountains and in the moist canyons around Salt Lake City, Utah. It has also been taken at Zion National Park, Utah (Creighton leg. and Coll.); Maggie Basin, Nev. (F. M. Gaige leg.; UMMZ); Lehman Caves, Mt. Wheeler, Nev. (Creighton leg. and Coll.); and Pole Canyon, East Humboldt Mts., Nev. (Creighton leg. and Coll.).

At Moscow Mountain (Idaho), Yellowstone Park, and the San Francisco Peaks (Ariz.), where I was able to study large populations first-hand, I found this species most abundant in the fir-yellow pine transition, sparser in the middle third of the fir belt, and rare in the upper third of the fir belt. Below the fir it extends into the pure pine forest and may be locally abundant there, even under relatively dry conditions.

ECOLOGY. My own studies of *sitkaensis* in the field, combined with abundant field notes supplied me by A. C. Cole, Kenneth Kraft, G. C. Wheeler, and others, show that this species is primarily a forest dweller, nesting in rotting logs and stumps and under stones. It penetrates forest clearings secondarily and

is abundant, at least locally, in the almost treeless plains of central and western North Dakota (P. B. Kannowski, Joe Davis, R. P. Uhlmann; material in G. C. Wheeler Coll. and UMMZ) and southern Idaho (A. C. Cole). In the latter situation it usually nests under stones but occasionally constructs irregular soil craters removed from any ground cover. At Moscow Mountain, Idaho, I found hundreds of nests in rotting wood and under stones within the forest margin, but only one associated with a crater in open soil. In Itasca State Park, Minn., Kraft found six colonies associated with craters, out of sixteen collected. Cole, in collecting *Lasius* from a wide diversity of habitats in New Mexico, took *sitkaensis* most consistently under stones in moist, shaded soil. At Cloudcroft, New Mexico, and the San Francisco Peaks, Arizona, I found the species most abundant well back in the shaded portions of the forest, nesting almost exclusively under stones. In the White Mountains of New Hampshire, however, *sitkaensis* populations are densest nesting under stones in overgrown meadows on the lower slopes, and are less abundant under stones in the adjacent spruce-fir-larch forest.

Local populations of *sitkaensis* and its relatives *neoniger*, *alienus*, and *crypticus* are often spectacularly dense. It seems inevitable that some amount of interspecific competition must result, and it is therefore not surprising to find a tendency for these species to replace one another ecologically where they occur together. Near Bemidji, in central Minnesota, I found *sitkaensis* in a deciduous woodlot nesting in rotting logs and stumps, a niche usually occupied by *alienus* in localities farther east where *sitkaensis* is rare or absent. *Neoniger* prevailed in adjacent open areas. - At Kiowa, Montana, *sitkaensis* again seemed to replace *alienus* in deciduous woods; *crypticus* was abundant in an adjacent subalpine meadow, while *neoniger*, its nearest ecological equivalent, was absent. At Moscow Mountain and Cloudcroft, *sitkaensis* occurred in exceedingly large numbers, apparently to the exclusion of other members of the subgenus.

The food habits of *sitkaensis* are evidently generalized. Kannowski (*in litt.*) has found workers on several occasions associated with aphids in galleries under rocks, while at Moscow Mountain I observed workers carrying dead and crippled insects back to their nests during the early part of the night. A

colony maintained under observation at the Harvard Biological Laboratories for nearly two years has readily accepted both honey and dead and crippled insects.

Winged forms have been taken in the nests from July 4 (Neche, Pembina Co., N. Dak.; E. L. Krause leg.; G. C. Wheeler Coll.) and July 7 (Cloudcroft, N. Mex.; W. M. Wheeler leg.; MCZ) to September 24 (Lodema, Pembina Co., N. Dak.; Krause leg.; G. C. Wheeler Coll.). The great majority of *in nido* records are from August. G. C. Wheeler took pairs flying in copula at Marblehead, Mass., on September 3, 1927, and N. A. Weber took a pair in copula at Towner, McHenry Co., N. Dak., on August 18, 1927 (both G. C. Wheeler Coll.). Eidmann (1933) observed nuptial flights of "*americanus*" (probably the *sitkaensis* already referred to) in the Matamek region of Quebec on September 4. Borys Malkin found stray dealate queens at Wrangell, Alaska, in the first week of August.

Lasius brunneus (Latreille)

(Subg. *Lasius*)

Formica brunnea Latreille, 1798, Essai Fourmis France, p. 41; worker; original description. Type locality: France.

Formica pallida Latreille, 1798, *ibid.*, p. 41; worker; original description. Type locality: France. NEW SYNONYMY.

Formica brunnea var. *pallida*, Latreille, 1802, Histoire Naturelle des Fourmis, p. 169.

Lasius niger var. *alieno-brunneus* Forel, 1874, Les Fourmis de la Suisse (Nouv. Mem. Soc. Helv. Sci. Nat.), p. 47; worker; original description. Synonymized by Stärcke, 1944, Ent. Ber., **11**: 156–157.

Lasius niger brunneus var. *himalayana* Forel, 1894, Jour. Bombay Nat. Hist. Soc., **8**: 404; worker; original description. Type locality: Himalayan Mts., 6000–9000 feet. NEW SYNONYMY.

Lasius niger var. *himalayanus*, Forel, 1917, Bull. Soc. Vaud. Sci. Nat., **51**: 725.

Acanthomyops brunneus var. *nigro-brunneus* Donisthorpe, 1926, Ent. Rec., **38**: 18; worker. Type locality: Italy. NEW SYNONYMY.

DIAGNOSIS. A distinct species characterized by large males with intermediate *sitkaensis-niger* type mandibles and workers with short scapes and sparse pilosity.

Worker. (1) Scape shorter relative to head width than in

any other member of the subgenus (Fig. 5); SI 82-91 in all European series measured; 94 in the *himalayanus* lectotype and in one specimen from Lahore, Pakistan, both small specimens (see under geographic variation).

(2) Small individuals (PW 0.50-0.57 mm.), when viewed in perfect full face, with the lateral margins of the eyes not reaching the lateral borders of the head; in *niger* and *alienus* they reach or exceed it.

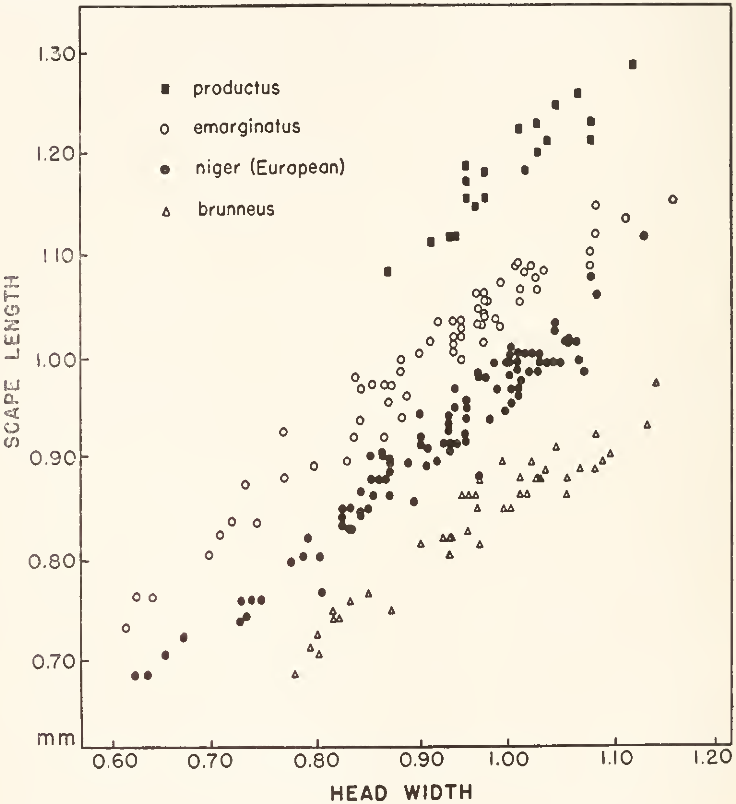


Fig. 5. Head width-scape length relationships in the worker caste of *L. brunneus* and the members of the *L. niger* complex. Further explanation in the text. Nest series chosen at random; no more than three workers per series were measured.

(3) Mandibles proportionately shorter, more incurved, and inserted slightly closer to the midline, and head more massive relative to the alitrunk, than other *Lasius s. s.* (Pl. 1, Fig. 9). Occipital margin viewed in full face flat to feebly convex, as opposed to the typically concave outline of *niger* and *alienus.*

(4) Mandible with only two basal teeth in all of seven nest series examined for this character.

(5) Scapes and tibiae completely devoid of standing hairs and nearly devoid of hairs of any inclination. Body pilosity sparse; the curving portion of the occipital angles viewed in full face typically devoid of hairs, rarely with one or two; the latter condition occurs in other members of the subgenus but is highly exceptional.

(6) Alitrunk and petiole homogeneous light reddish brown, rarely medium reddish brown, contrasting against the dark brown gaster. The head usually the same color, occasionally darkening to medium or dark reddish brown to contrast against the alitrunk. (*Niger* and *alienus* typically concolorous.)

Queen. (1) SI low; 68-71 in 9 individuals from 6 localities having HW 1.49-1.64 mm., and 76 in a smaller individual with HW 1.39 mm.

(2) Pilosity and mandibular dentition as in worker.

(3) Frontal suture well marked, set in the middle of a conspicuous broad, shallow trough.

(4) Color distinctive; body uniformly dark reddish brown, appendages a contrasting yellowish brown.

(5) Fore wings infumated in the inner and upper thirds.

Male. (1) Larger than other members of the subgenus, HW 1.04-1.10 mm.

(2) Mandibles of a type intermediate between *sitkaensis* and *niger:* there is a well marked subapical cleft as in *sitkaensis,* but it is set more posteriorly than in this primitive species; the basal angle is broadly rounded and the masticatory border lacks denticles, both of which characters are associated with the more advanced *niger* type.

(3) Frontal suture conspicuous as in queen.

(4) The entire dorsal petiolar margin involved in a deep concavity. In a series from Windsor Forest, Berks, England, secondary lateral convexities are present within this concavity.

(5) Parameres shorter relative to HW than in other members of the subgenus (Fig. 7).

FURTHER DESCRIPTION. *Worker.* Size range and dispersion probably about the same as in *niger.* In a sample of 29. with no more than 2 individuals per nest series, PW range 0.50-0.73 mm., mean with standard error 0.630 ± 0.012 mm., standard deviation 0.063 mm. ML less than EW. Anterior margin of median clypeal lobe and structure of the mandibular basal angle essentially as in the *niger* complex. The greater massiveness of the alitrunk in this species can perhaps best be expressed as a ratio of alitrunk length to the maximum head depth measured perpendicular to the long axis of the head. Several medium-sized *brunneus* gave such a ratio of 67-69, whereas *alienus* of comparable size ranged between 70 and 76. Viewed from the side the propodeal angle tends to be more acute and the declivitous face of the propodeum tends to be longer relative to the dorsal face than in other *Lasius s. s.* The dorsal margin of the petiole was invariably concave in all series examined; occasionally the concavity is so deep as to be nearly semicircular.

Male. SI of several individuals measured 60-64, overlapping part of range of variation of *niger* (*q. v.*). ML 0.15-0.17 mm., overlapping part of ranges of *niger* and *emarginatus.*

GEOGRAPHIC VARIATION. Series examined were too limited in number and distribution to give a clear picture of geographic variation. One trend is suggested by the fact that two of the three Asiatic specimens examined had a SI above the range of variation of the European sample; these were a single specimen from Lahore, Pakistan, and one of two *himalayanus* syntypes.

DISTRIBUTION. *Brunneus* is widely distributed in western Europe, reaching south to North Africa and eastward to the western Himalayas. Below are listed the records which have been verified in the course of the present revision.

ENGLAND: Windsor Forest, Berks (H. Donisthorpe leg.; specimens in MCZ, USNM, and several private European collections); Chadbury, Worcestershire (C. S. Collingwood leg. and Coll.). NORWAY: Ullern, near Oslo (H. Holgersen leg. and Coll.). SWEDEN: Stockholm (K.-H. Forsslund leg. and Coll.). SWITZERLAND: Flawil (H. Kutter leg. and Coll.); Aarau

(Kutter Coll.); Freiburg (A. Forel leg.; MCZ). AUSTRIA: Vienna Forest (Wiener Wald) (MCZ). ITALY: Lipizza, near Trieste (B. Finzi leg.; MCZ). YUGOSLAVIA: "Podcetrtek" (not located) (Jaeger leg.; Holgersen Coll.); Bosnia (Reitter leg.; Holgersen Coll.). ALBANIA: Mali Daiti (Ravasini and Lona leg.; MCZ). U.S.S.R.: Krimea (W. Karawajew; MCZ). ALGERIA: no further data (Reitter leg.; Holgersen Coll.). PAKISTAN: Lahore (R. K. Enders leg.; Weber Coll.).

This species has been confused so often with *L. alienus* that literature records are of dubious value. Two have been encountered which are nevertheless of sufficient interest to deserve mention here: Puenta de la Reina, Navarra, Spain (Santschi, 1919); and Enzeli (Pehlevi), Iran (Crawley, 1920). These represent slight range extension if valid.

ECOLOGY. Most European authors agree that *brunneus* is a timid species adapted to living under the bark and in the wood of tree trunks. Donisthorpe (1927) found a large population of this species in the Windsor Forest of England limited to living trees, which the ants penetrated from the trunk up into the main branches and down into the roots. Various trees were inhabited, including oaks, elm, ash, beech, poplar and maple. It is not clear whether the workers carried on much excavation in the living wood, but this seems unlikely due to the rather unspectacular mandibular apparatus of the species. Forsslund (1949) found *brunneus* in oaks in dense, undisturbed woodland in several localities in the vicinity of Stockholm. The nests were mostly in dead wood, but occasional galleries penetrated living wood. Scherdlin (1909) found the species in Alsace nesting in the trunks of trees and timber of houses. Clausen (1938) observed a swarm of reproductives inside a house in Zurich. Gösswald (1932) states that in Germany *brunneus* is found as often under stones as in dead wood; since this observation is divergent from those of other authors, the possibility must be considered that he was erroneously including some *alienus* in his concept of *brunneus*.

Donisthorpe (*ibid.*), who has undertaken the most careful study of this species to date, found workers transporting and tending aphids of the genus *Stomaphis*. He also observed them carrying psocids and other small insects to the nests, presumably for use as animal food.

Brunneus appears to hold its nuptial flights earlier in the day and season than other European members of the subgenus. Donisthorpe (*ibid.*) encountered winged queens and males swarming over the trunk of an oak at noon on June 25, and Forsslund (*ibid.*) saw the same thing from noon to 1:30 p.m. during the period June 10-16.

SYNONYMY. *Formica pallida* Latreille and *Acanthomyops brunneus* var. *nigro-brunneus* Donisthorpe appear to represent the two extremes of normal color variation in *brunneus* and to be without any geographic significance.

Lasius brunneus var. *himalayanus* Forel. Lectotype by present selection, a worker in the AMNH. PW 0.56 mm., HW 0.78 mm., SL 0.73 mm., SI 94. A syntype presumably from the lectotype nest series has been placed in the MCZ and gives the following measurements: PW 0.64 mm., HW 0.97 mm., SL 0.86 mm., SI 89, ML 0.17 mm., EW 0.19 mm. The differences in size, color and pubescence given by Forel are actually insignificant. The lectotype and syntype seem to be well within the normal range of variability of European *brunneus* in every character with the one exception of the high SI of the lectotype.

[Lasius schiefferdeckeri Mayr]
(Subg. *Lasius*)

Lasius schiefferdeckeri Mayr, 1868, Beitr. Naturk. Preuss., Phys.-ökon. Ges. Königsberg, 1: 44–46; pl. 1, fig. 2; pl. 2, figs. 27–32; worker, queen, male; original description.

Lasius edentatus Mayr, 1868, *ibid.*, pp. 46–47; male; original description. NEW SYNONYMY.

Lasius schiefferdeckeri, Wheeler, 1914, Schrift. Phys.-ökon. Ges. Königsberg, **55:** 120.

DIAGNOSIS. This is the predominant *Lasius* of the Baltic amber deposits. Wheeler (1914) offered the opinion that *schiefferdeckeri* is very close to the modern species *L. alienus* ("*niger* var. *alienus*" and "*americanus*"), differing only by its smaller size. The present study has shown that size differences are actually insignificant but that *schiefferdeckeri* does exhibit variation in scape index transspecific for most of the modern members of the *niger* complex, as well as a peculiar male mandible struc-

ture intermediate between the primitive *sitkaensis* type and advanced *niger* type.

Worker. (1) Size range and mean, clypeus, mandibular dentition, and appendage pilosity similar to *alienus*.

(2) ML exceeding EW.

(3) SI very variable, ranging in value from typical *emarginatus* through typical (northern European) *niger* to typical *brunneus*.

Queen. No specimens were seen during the present study. A figure of the head by Mayr is somewhat diagrammatic but shows a *niger*-type clypeus and mandibular dentition as opposed to the distinctive *sitkaensis* types.

Male. (1) Very small, at lower limit of *alienus* size variation.

(2) Mandible form showing great variation which brackets both the *sitkaensis* and *niger* types, a condition also encountered in the modern species *L.* (*Cautolasius*) *flavus* (see under further description of *schiefferdeckeri* below).

SYNTYPES. The only specimens designated as types by Mayr were several males inclosed in a single piece of amber in the Menge Collection (Leipzig). These were given as the source of his male diagnosis ("Typen bei der Diagnose") and described as having denticulate mandibles. From this information and by inference from comparison with the description of *L. edentatus,* we may assume that these males had *sitkaensis*-type mandibles, with a well defined basal angle and denticulate masticatory border, which characters can now be shown to fall at one extreme of the *schiefferdeckeri* variation.

MATERIAL STUDIED. Eleven workers and three males in the William A. Haren Collection (MCZ).

FURTHER DESCRIPTION. In the present study each piece of amber was planed and polished at several angles to allow precise measurement of the essential structures. As a result, descriptions of these fossil specimens are probably nearly as accurate as those of modern material, and their status relative to modern species can be discussed with some confidence.

Worker. Individual measurements of each of the eleven workers are given in the accompanying table. It will be noted that even in this small sample the scape index is extraordinarily

Variation in Critical Characters in *Lasius schiefferdeckeri* Mayr (Workers)

Specimen	PW (mm.) (or estimate of size)	$\frac{SL}{HW}$	SI	SI regression line fit	ML (mm.)	dentition	anterior clypeal border	seta count
1	very small, lower *alienus* limit			approaching *brunneus*		*niger*-type (probably only 2 basal teeth)		0?
2	0.50							1
3	0.46	$\frac{0.71}{0.68}$	105	*niger* lower limit	0.18 (EW=0.14)			0
4	0.69	$\frac{0.96}{0.93}$	103	*niger* upper limit	0.21 (>EW)			0
5	0.50	$\frac{0.83}{0.77}$	108	*niger-emarginatus* int.		*niger* type		0?
6	0.43	$\frac{0.60}{0.69}$	87	*brunneus*				0?
7	0.64	$\frac{0.92}{0.86}$	107	*niger-emarginatus* int.	0.22 (EW=0.21)	*niger* type (only 2 basal teeth)	*niger* type	0
8	0.61	$\frac{0.87}{0.93}$	94	*niger-brunneus* int.				0
9	small	$\frac{0.80}{0.66}$	121	*emarginatus*				0
10	0.54	$\frac{0.84}{0.84}$	100	*niger*	EW(?)			0
11	0.48	$\frac{0.87}{0.83}$	104	*niger-emarginatus* int.	EW(?)			

variable in comparison to modern species. That we are dealing with a single species in the amber material is evidenced by the lack of any tendency to grouping in the SI values, plus the uniformity of the palpal and pilosity characters. For instance, in no. 3, a low SI is combined with a high ML, and in nos. 5, 7, and 9, a high SI is combined with *alienus*-like pilosity; both situations are consistent with the reminder of the sample but unlike anything found in modern populations.

Characters additional to those in the chart may be mentioned. The CI is 100 in no. 6, 93 in no. 7, 89 in no. 9, 95 in no. 10, and 88 in no. 11. This also represents an unusual amount of variation for a single species, even when the considerable amount of overlap betwen the regression zones of modern species is taken into account. The SI and CI are concordant in every case but no. 9, which has an *emarginatus* SI and *niger* CI. The dorsal margin of the petiole seen in frontal view shows the same type of variation as in modern members of the subgenus, ranging from weakly concave to weakly convex.

Male. Specimen no. 1. Subapical cleft of mandible present but shallower than in *sitkaensis;* masticatory border flat; basal angle intermediate in development between *sitkaensis* and *niger.* HW 0.77 mm., SI 85. SI very high with respect to modern members of the subgenus, above the *emarginatus* range but still below that of *productus.* Paramere similar in proportionate size and shape to that of *alienus.*

Specimen no. 2. Mandible partly decomposed and further obscured by a fissure, apparently with a well-developed spical cleft and basal angle. Size somewhat smaller than no. 1. Paramere similar in proportionate size and shape to that of *alienus.*

Specimen no. 3. Subapical cleft present but set about one-third back from the apex, an intermediate *sitkaensis-niger* condition occasionally seen in *L. flavus* and rarely in *L. alienus.* Basal angle weakly developed, close to *niger* type. HW *ca.* 0.66 mm.

The diagnostic character given for *L. edentatus* Mayr, based on a single amber male, was the absence of denticulae and distinct basal angle on the mandible. I have synonymized this species on the assumption that the great variability in the male mandible in the three specimens just described and the intermediate *sitkaensis-niger* condition of two of them indicates total

variability similar to that seen in *flavus,* i.e. ranging from the *sitkaensis* type all the way to a condition closely approaching the *niger* type. In fact, the three specimens by themselves encompass about three-fourths of the total possible variation. I cannot attach any significance to the fact that Wheeler himself failed to find such a transition in the 20 males he examined. When he states ''I have found no specimens agreeing with this description [*edentatus*], either in the Geolog. Inst. Koenigsberg Coll. or in the Klebs Coll.'', he is giving the unintentional but erroneous impression that all 20 specimens were examined for the diagnostic character. Actually, he was probably unable to see the mandible outline in the majority of specimens he examined. Nearly every specimen in the already-prepared Haren material which I studied had to be reground and repolished before a favorable view was obtained; there is no evidence that Wheeler ever made preparations of this sort during his own study.

FAUNAL RELATIONSHIPS. *L. schiefferdeckeri* was apparently one of the most abundant ants of Baltic amber times, since it composed 1172 out of the 11,678 amber specimens collectively studied by Mayr, André, and Wheeler (Wheeler, 1914). It was surpassed in this respect only by *Iridomyrmex goepperti* (Mayr), *I. geinitzi* (Mayr), and *Formica flori* Mayr. Wheeler found workers included in the same block of amber with *Iridomyrmex goepperti* and *Formica constricta.* In the absence of further data it may be contended that *Lasius schiefferdeckeri* was a member of a warm temperate fauna, possibly segregated by elevation or latitude in the extensive amber forest region. Its presumed derivative species, the members of the modern *niger* complex, have continued to thrive in the Palaearctic Region, along with species of *Stenamma, Leptothorax, Formica,* and *Prenolepis,* at the same time that numerous other amber genera have withdrawn to tropical regions or declined to total extinction.

[LASIUS PUMILIS Mayr]
(Subg. *Lasius*)

Lasius pumilis Mayr, 1868, Beitr. Naturk. Preuss., Phys.-ökon. Ges. Königsberg, 1: 46; pl. 2, fig. 33; worker; original description.

Lasius punctulatus Mayr, 1868, ibid., p. 46; pl. 2, fig. 34; queen; original description. NEW SYNONYMY.

Lasius pumilis, Wheeler, 1914, Schrift. Phys.-ökon. Ges. Königsberg, **55:** 122–123.

Lasius pusillus [!], Wheeler, 1914, *ibid.,* p. 142.

DIAGNOSIS. A tiny Baltic amber species with no close living relatives. The worker caste resembles superficially that of the modern species *L. sitiens* Wilson but can be distinguished from it readily on the basis of palpal and dentition characters.

Worker. (1) Exceedingly small, PW under 0.30 mm. in the two specimens examined.

(2) Alitrunk completely lacking standing hairs.

(3) Funicular segments II, III, and IV slightly broader than long. Length of maxillary palp segment VI (ML) exceeding the EW.

(4) Mandibles with only one basal tooth in the single specimen which could be examined for this character.

Queen. Assuming that *punctulatus* is the queen of *pumilis,* as all the evidence seems to indicate, this caste is distinguished from that of all other *Lasius s. s.* by its extremely small size. Total length, according to Mayr, 3.0-3.8 mm.

SYNTYPES. Three specimens were mentioned by Mayr in the original description, one each in the Königsberg Geological Institute Collection, Menge Collection, and Mayr Collection.

MATERIAL EXAMINED. Two workers in the William A. Haren Collections (MCZ).

FURTHER DESCRIPTION. *Worker.* Specimen no. 1. PW 0.30 mm., HW 0.46 mm., SL 0.48 mm., SI 105, CI 92, ML 0.11+ mm., EW 0.10 mm. Funicular segments II, III, IV broader than long. ML exceeding the maximum width of the fore tibia, thus markedly longer than in the small modern species *sitiens.* Eye with only 12 ommatidia but not noticeably reduced proportionate to total head size. Mandibles relatively small, giving the head an unusually rounded appearance when viewed in full face. Anterior margin of the median clypeal lobe with straight lateral faces but with a broadly rounded middle so that an outline intermediate between the *niger* and *neoniger* conditions is obtained. Petiole broadly spatulate in frontal view, with gradually rounded dorsal corners and flattened dorsomedian margin.

Specimen no. 2. HW 0.41 mm., SL 0.45 mm., SI 109, CI 93, ML 0.14 mm. (greater than estimated EW). Funicular segments II, III, and IV broader than long. Mandibular dentition of elementary formicine type (see under Terminology and Measurements) but with only one basal tooth.

A conflict exists between Mayr's description and figure of this species: funicular segments II, III, and IV are stated to be broader than long, but the figure shows II and III longer than broad. The description is probably more accurate, as indicated by the two specimens measured in the present study.

[Lasius peritulus (Cockerell)]
(Subg. *Lasius*)

Tetramorium peritulum Cockerell, 1927, Ann. Mag. Nat. Hist., (9) **19**: 165; male; original description.

Lasius peritulus, Carpenter, 1930, Bull. Mus. Comp. Zool., **70**: 58.

DIAGNOSIS. This is the *Lasius s. s.* species of the Florissant shales, which deposits are considered lower to middle Oligocene in age (MacGinitie, 1953) and the best North American counterpart of the Baltic amber so far as the preservation of insects is concerned. I have had the opportunity to study the excellent collection of *peritulus* arranged by Prof. F. M. Carpenter at the Museum of Comparative Zoology at Harvard University. Despite the fact that these specimens represent finely preserved rock fossils, they are still far inferior to the amber material and cannot be determined accurately beyond placement within the *niger-neoniger* species group.

Queen. Of 129 specimens examined, 5 were in a position to show the basal angle of the mandible, which is the crucial diagnostic structure in the subgenus. Each of the 5 possessed a "*niger*-type" mandible (see under description of *niger*), with the basal tooth as large as the adjacent teeth and aligned with them. Although the material is too badly crushed to allow precise measurements, the total size appears small, toward the lower limit of the range of size variation in *niger*.

Male. Of 91 specimens examined, 5 showed the entire mandibular outline. In each case this was unmistakably the "*niger* type", with the masticatory border shallowly impressed in its distal half, the basal angle broadly rounded, and the preapical

cleft lacking. Two other specimens showed only the basal angle, which was also broadly rounded. The total size is approximately the same as for the modern Nearctic populations of *niger* and *alienus*.

HOLOTYPE. According to Carpenter, the unique type is a well preserved male now located in the British Museum.

Lasius niger (Linnaeus)
(Subg. *Lasius*)

Formica nigra Linnaeus, 1758, Syst. Nat., Ed. 10, **1**: 580; worker; original description. Type locality: Europe.

Lasius niger, Fabricius, 1805, Systema Piezatorum, p. 415.

Lasius niger var. *alieno-niger* Forel, 1874, Les Fourmis de la Suisse (Nouv. Mem. Soc. Helv. Sci. Nat.), pp. 47, 49; worker, queen; original description. Type locality: Switzerland. NEW SYNONYMY.

Lasius niger aliena var. *alieno-nigra*, Emery, 1925, Genera Insect., fasc. 183, p. 230.

Lasius alienus alieno-niger, Zimmermann, 1930, Verh. Zool.-bot. Ges. Wien, **84**: 48.

Lasius niger var. *alienoides* Emery, 1891, Explor. Sci. Tunisie, Paris (Impr. Nat.), p. 16; worker; original description. NEW SYNONYMY.

Lasius niger flavescens Forel, 1903, Ann. Mus. Zool. Acad. Imp. Sci. St. Petersburg, **8**: 386–387; worker; original description. Type locality: Bukhara, Uzbek S. S. R., Soviet Central Asia; by present selection. NEW SYNONYMY.

Lasius niger emeryi Ruzsky, 1905, Formicariae Imperii Rossici (Schrift. Naturforsch.-Ges. Univ. Kasan, vol. 38), pp. 313–314; worker; original description; In Russian. Type locality: Pamirs, Tadzhik S. S. R., Soviet Central Asia. NEW SYNONYMY.

Acanthomyops niger nitidus Kuznetzov-Ugamskij, 1927, Rev. Russ. Ent., **21**: 188; worker; original description. Type locality: Kara-su River, 65 km. northeast of Tashkent, Uzbek S. S. R., Soviet Central Asia. NEW SYNONYMY.

Acanthomyops niger alienus var. *pilicornis* Kuznetzov-Ugamskij, 1927, *ibid.*, p. 189; worker; original description. Type locality: Zailiski Ala Tau Mountains, near the city of Alma Ata, Kazakh S. S. R., Soviet Central Asia. NEW SYNONYMY.

Acanthomyops niger var. *minimus* Kuznetzov-Ugamskij, 1928, "Ants of the South Ussuri Region" (in Russian), U.S.S.R. National Geographic Society Publications, p. 20; worker; original description. Type locality: Okeanskaja Railroad Station, near Vladivostok, Soviet Maritime Territory. NEW SYNONYMY.

Lasius emarginatus var. *nigrescens* Stitz, 1930, Mitt. Zool. Mus. Berlin, **16:** 240; queen; original description. Type locality: Maz, Westl. Täler, Pamirs, Tadzhik S. S. R., 3580 meters. NEW SYNONYMY.

Lasius niger coloratus Santschi, 1937, Bull. Ann. Soc. Ent. Belg., **68:** 387; worker, queen; original description. Type locality: Musha, Formosa; virtual selection by Santschi, 1941, ref. below. NEW SYNONYMY.

Lasius emarginatus var. *japonicus* Santschi, 1941, Mitt. Schweiz. Ent. Ges., **18:** 277–278; worker; queen; original description. Type locality: Tokiawa, Hokkaido; by present selection. NEW SYNONYMY.

Lasius transylvanica Röszler, 1943, Zool. Anz., **144:** 44–46; worker, male; original description. Type locality: Nyárádtö, Rumania. NEW SYNONYMY.

Lasius transsylvanicus [!], Stärcke, 1944, Ent. Ber., **11:** 157.

Lasius niger neoniger, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 420, *part.* [*nec neoniger* Emery 1893].

DIAGNOSIS. The worker is best distinguished by its abundant standing appendage pilosity combined with the clypeal outline and mandibular dentition characteristic of the "*niger* complex" (*niger, alienus, emarginatus, productus*). Over most of Europe and in western North America *niger* has a scape index regression zone intermediate between those of *brunneus* and *emarginatus,* but in peripheral Eurasian populations this zone shifts to overlap that of *emarginatus.* The male is best distinguished by the possession of abundant standing pilosity on the appendages combined with the "*niger* type" mandible described below.

Worker. (1) More than 95 per cent of the workers within HW range 0.61-1.21 mm., exclusive of material from North Africa, the Balearics, Azores, Madeira, and eastern Asia, possess a SI between 95 and 103. This is a strongly allometric character (Fig. 5), with minimas (HW less than 0.61 mm.) ranging up to 109.

(2) As a corollary to (1), ML within this sample exceeds EW.

(3) Mandibular dentition characteristics of the *niger* complex: basal teeth two to four in number, equal in size, and spaced at even intervals; opposed to the *neoniger* complex, in which the two or three basal teeth are irregularly spaced and the central one of a set of three is often reduced in size.

(4) Clypeus characteristic of the *niger* complex: when the mandibles are opened and the head is viewed in perfect full face, the anterior border of the median clypeal lobe describes an even,

broad parabolic curve, with the sides at least feebly convex and only occasionally meeting in a point at the midline; opposed to the more angular clypeal border of the *neoniger* complex. (See Pl. 1, Figs. 2 and 3.) The clypeus is usually, but not always, keeled.

(5) Scapes and tibiae always with abundant standing pilosity, except in minimas with PW less than 0.47 mm. The inclination and density of this pilosity show striking geographic variation (see below). In general, *niger* complex workers with seta counts greater than 25 are almost certainly *niger,* but those with less might be *alienus* and should be determined with the aid of the allometry regression zones plotted in Figure 6.

Queen. (1) Within the geographic limits stated in the first worker character above, queens with HW between 1.54 and 1.82 mm. have an SI between 72 and 80.

(2) As a corollary to (1), queens within this sample have a ML between 0.17 and 0.23 mm., with over 90 per cent falling within 0.18-0.21 mm.

(3) Clypeus and mandibular dentition as in worker.

(4) Scapes and fore tibiae with abundant standing hairs; seta count usually over 20 and often over 40. Inclination and density subject to geographic variation as in worker.

(5) Wings hyaline except for a small area distal to the axillary sclerites; this is a general *niger* complex character.

Male. (1) Within the geographic limits stated in the first worker character above, SI 62-69, ML 0.14-0.16 mm.

(2) Mandible characteristic of the *niger* complex: primitive preapical cleft of *sitkaensis* and *brunneus* modified into a shallow angular depression placed centrally on the masticatory border or lacking altogether, so that the masticatory border curves gently inward from the apex and then outward to meet the basal border. The basal angle broadly rounded, the masticatory border curving gradually into the basal border. Denticles lacking on the masticatory border. (See Pl. 1, Fig. 5.)

(3) The subgenital plate subrectangular, the posterior sclerotized, setiferous lobes not more than one-fourth as wide across their base as the plate itself but protruding past the unsclerotized posterior rim and reaching as far back as the level of the tips of the posterolateral flanges. A single series from Shriek, Belgium (A. Raignier leg.; MCZ), contains individuals with two

distinct lobes, a single lobe, and several stages intermediate in the coalescence of two lobes.

(4) Long standing hairs present over most of the surfaces of the scape and fore tibia, but much sparser than in the worker and queen; seta count usually less than 5.

(5) Size (see under geographic variation).

FURTHER DESCRIPTION. *Worker.* In a sample of 165, with no more than 2 per nest series, PW range, 0.40-0.83 mm., mean with standard error 0.630 ± 0.005 mm., standard deviation 0.069 mm.

Thirty-four individuals each representing a different nest series were examined especially for dentition; 27 had three basal teeth, 5 had four, and 2 had four with the antepenultimate tooth reduced in size; one lacked the second intercalary tooth.

Petiole outline more variable than in other members of the subgenus. Among 52 nest series examined especially for this character, the dorsal border was gently convex in 14, straight in 11, roundly concave in 22, and angularly concave in 5.

In a strong, reflected, artificial light, the body surface is subopaque to moderately shining. The degree of shininess varies inversely with the density of the pubescence and coarseness of the shagreened sculpturing, both independent and highly variable characters by themselves.

Body nearly or completely concolorous medium to blackish brown. Legs typically medium brown, scapes tending to yellowish brown.

GEOGRAPHIC VARIATION. Some amount of geographic variation has been found in appendage pilosity, appendage length, male size, and male genitalia, each of which appears to be genetically controlled and independent of the others.

Appendage pilosity. Throughout Europe, North Africa, and the adjacent Atlantic Islands, quantity of standing appendage pilosity varies in an allometric regression zone relative to head width as shown in Figure 6. This zone is sufficiently discrete from that of the sibling species *alienus* to allow a certain placement of nearly all of the enormous numbers of nest series examined during the present revision. In eastern Asia two changes occur in this character. If series from northern and western China, Manchuria, Korea, and Japan are plotted as a unit, the regression zone is seen to have shifted so that its lower end is

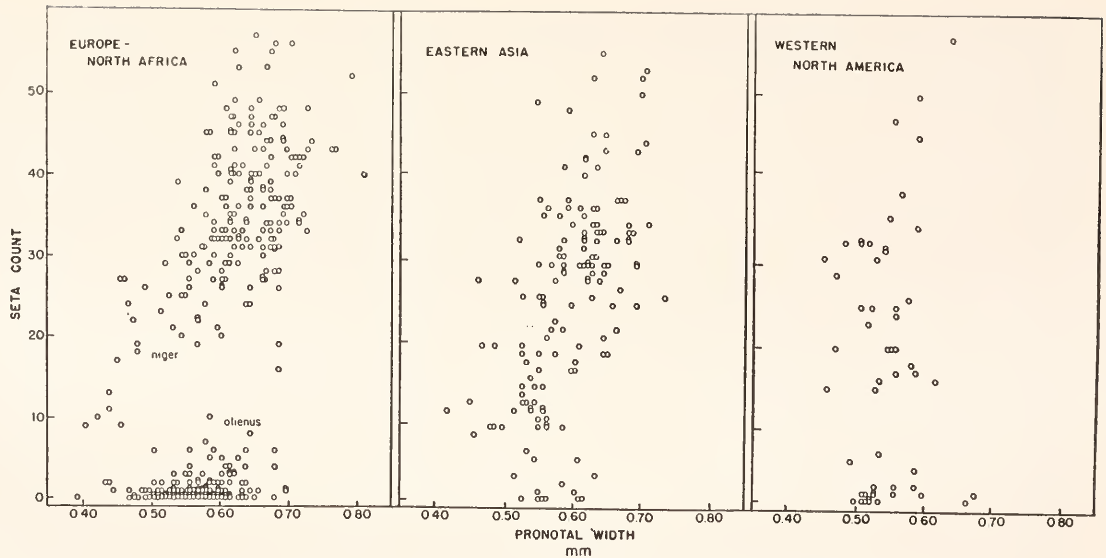


Fig. 6. Pronotal width-seta count relationships in the worker caste in three geographic samples of *L. niger* and *L. alienus*. This is the principal character used to separate these two closely related species. Further explanation in the text. Nest series chosen at random; no more than three workers per series were measured.

contiguous with and possibly overlapping the *alienus* zone (see also Fig. 6). As a result east Asian nest series comprised of smaller individuals (PW 0.47-0.59 mm.) often cannot be determined with assurance as either *niger* or *alienus*. In view of several other striking cases, in *Lasius,* of species convergence as a result of geographic variation, I do not think that this particular case is best interpreted as having arisen through interspecific hybridization, although this explanation is certainly available. Rather, I consider it significant that *alienus* is much rarer in Asia than in Europe, and it is my personal view that *niger* converges morphologically toward *alienus* in Asia because it is allowed to penetrate more of the usual *alienus* ecological niches there. No direct evidence is available to support such a view, but there does exist a fairly well documented precedent, to be described later, in the relationship between *Lasius flavus* and *L. nearcticus*.

Unfortunately, geographic variation in the seta count cannot be plotted precisely, locality by locality, on the basis of available material, because it is necessary for a given nest series to fall in the higher size range to show which regression zone it fits. Moreover, at least several individuals are needed to judge the character of the colony as a whole. About the most that can be said is that the seta count convergence appears to predominate in northeastern Asia, while lack of material makes it impossible to determine its westward extension. I have noted it in a single specimen from Naran, N. W. F. P., Pakistan (R. K. Enders leg.; Weber Coll.). One series each from Hu Hsien and Miao T'ai Tze, Shensi Prov., China (W. L. Brown leg.; MCZ) conform to the European population. Alate queens from Beh Luh Din, Szechwan Prov., China (D. C. Graham leg.; USNM) have relatively sparse appendage pilosity and may therefore conform to the northeastern Asian population.

In the mountains of western North America, *niger* exhibits a regression zone very similar to that of the northeastern Asian population, as shown in Figure 6. The regression in fact may be even steeper, approaching an almost perpendicular slope.

Another, more conspicuous pilosity change occurs in southeastern Asia: the scape becomes densely clothed with decumbent to subdecumbent hairs 1/4 to 3/4 as long as the greatest width of the scape, forty or more being counted along the single plane used

in the seta count, and often dense enough to give a furry appearance. This character seems to predominate in Formosa and is occasional in Pakistan, Korea, Japan, and China. FORMOSA: Funkiko (3 series, F. Silvestri, J. Sonan, and L. Gressitt leg.; MCZ); Musha (*L. niger coloratus* Santschi cotypes); Rakuraku (S. Miyamoto leg.; Yasumatsu Coll.); Sakahen (Gressitt leg.; MCZ); Suisharyo (Gressitt leg.; MCZ). CHINA: "Yi Leang" (not located; Silvestri leg.; MCZ). KOREA: Suijen (Silvestri leg.; MCZ). PAKISTAN: Nathagali, N. W. F. P., 8200 feet (R. K. Enders leg.; Weber Coll.). JAPAN: Nagasaki (Michino-o), Kyushu (Silvestri leg.; MCZ); Hirooka, Shikoku (H. Okamoto leg.; Okamoto Coll. and MCZ). An intermediate condition, in which the oblique hairs decrease in number and the sub-erect and erect hairs increase, is seen in series from the following localities: Soochow, Kiangsu, China (N. G. Gee leg.; MCZ); Seoul, Korea (Yasumatsu Coll. and MCZ); Ikegawa, Shikoku (Okamoto leg. and Coll., MCZ); Okayama, Honshu (Silvestri leg.; MCZ); Hikosan, Kyushu (Yasumatsu leg. and Coll., MCZ).

Appendage length. Variation in this character shows a mosaic geographic distribution. As mentioned previously, most European material falls in the HW-SL regression zone illustrated in Figure 5. Material from the Balearics, Gibraltar, North Africa, and the nearby Atlantic Islands (Canaries, Madeira, Azores) plotted together as a unit form a zone nearly coinciding with that of *L. emarginatus* (same figure). Eastern Asian material is highly variable, showing in aggregate a zone overlapping most of that of the typical European *niger*, but with most of the measurements falling in an area between the *niger* and *emarginatus* zones. The North American population conforms to the typical European zone. Thus in going from the Atlantic Islands east across Eurasia to North America the scape index alternates high, low, high, low.

The queen scape index is closely correlated. Among six series examined from the Balearics and Canaries, for instance, the SI varied between 77 and 80 and the ML between 0.32 mm. and 0.40 mm. (HW 1.61-1.71 mm.). In twelve series from eastern Asia, the SI varied between 73 and 82 and the ML between 0.21 mm. and 0.27 mm. (HW 1.68-1.78 mm.).

The total distributional data for the appendage character can

be condensed as follows. Eight series of workers from several localities in the Canary Islands (Gran Canaria, La Palma, and Teneriffe; W. M. Wheeler leg.; MCZ) fall in the *emarginatus* zone; two (Gran Canaria and Teneriffe) fall intermediate between *emarginatus* and the European *niger*. Three series from San Miguel, Azores (W. M. Wheeler and A. Schatzmayr leg.; MCZ), one specimen from Madeira (MCZ) and four series from several localities in Mallorca and Minorca (W. M. Wheeler and H. Eidmann leg.; MCZ) fall in the *emarginatus* zone. Series

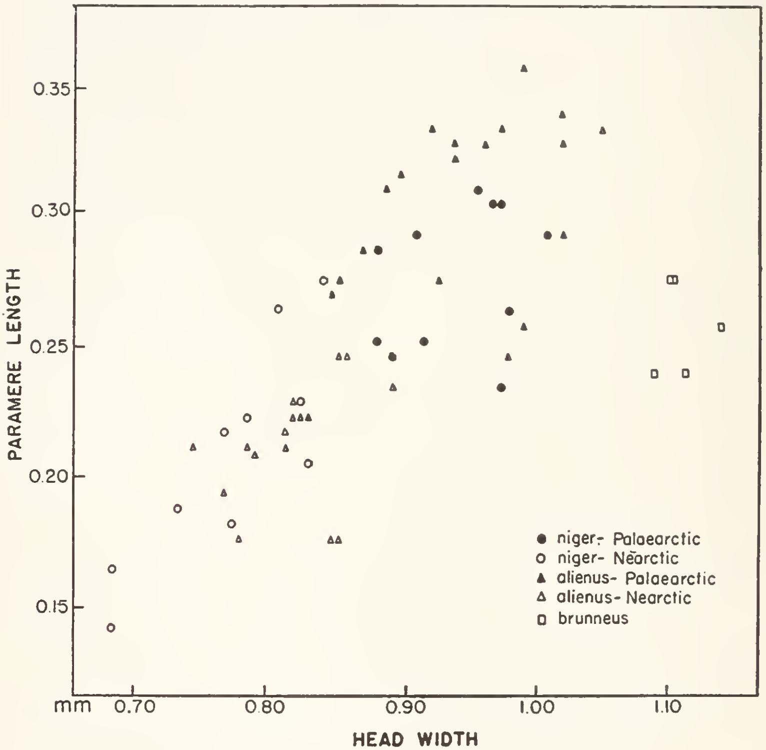


Fig. 7. Head width-paramere length relationships in the male caste of *L. brunneus* and two geographic samples of *L. niger* and *L. alienus*. Further explanation in the text. Nest series chosen at random; no more than two males per series were measured.

from Trolard-Taza, Algeria (Santschi leg.; USNM), and Azrou, Morocco, 1500 meters (Wheeler leg.; MCZ) are in the *emarginatus* zone, while one from Aïn Draham, Algeria (Heyler leg.; Santschi Coll.) is intermediate between *emarginatus* and the European *niger*. Other intermediate records include Centellas, Barcelona, Spain (de Xaxars leg.; MCZ); Lavarone, Venezia Tridentina, Italy (MCZ); Nabresina, Venezia Giulia (Ravasini leg.; MCZ); Mt. Capanne, Elba (Moczarski-Scheerpeltz leg.; MCZ). In general, one gains the impression that this character is clinal, grading away from centers in the Balearics and southern Spain eastward across southern Europe. It is noteworthy that the three series examined from Lebanon (see under distribution) fall in the European *niger* zone.

There is a gap in the data for most of the Middle East and central Asia. The specimen from Naran, Pakistan, previously mentioned falls at the upper extreme of the European *niger* zone, while one series each from Nathagali, Pakistan, and Schirparek, Afghanistan, are well inside the *niger* zone. Within the eastern Asian sample no geographic trend is evident. Series from peripheral localities in western China, Manchuria, and Hokkaido do not depart from the overall population trend toward an intermediate *emarginatus-niger* regression zone.

Male size. As shown in Figure 7, North American males are consistently smaller than those from Eurasia. No geographic trend within the populations of either continent was noted. This geographic pattern is exactly repeated in the closely related species *alienus* (*q. v.*).

Male genitalia. Fifteen males from three nest series from Los Tilos, Gran Canaria, have exceedingly thin parameres, outside the range of variation of the continental population. No other males from the Atlantic Islands have been seen, so that this character cannot be properly evaluated at the present time.

Summary of geographical variation. (1) In Europe the head width-appendage pilosity allometry regression zone of *niger* is well separated from that of its sister species *alienus*. In northeastern Asia and in North America the slope of the zone steepens, and its lower end comes to overlap that of the sympatric populations of *alienus* (Fig. 6). (2) In Formosa the appendage pilosity is denser and more oblique than elsewhere; the same character occurs sporadically throughout the rest of southern and eastern

Asia. (3) Appendage length, as measured by the scape index, exhibits an unusual pattern of alternating polytopic variation; the SI is higher in North Africa, the Balearics, Atlantic Islands (Canaries, Madeira, Azores), and eastern Asia, and lower in Europe and North America. (4) The males are consistently smaller in North America than in Eurasia. (5) The Canary Islands population may show a significant difference in paramere shape, but the data are as yet inconclusive.

DISTRIBUTION (see also Fig. 8). This species has the northernmost range of the four members of the *niger* complex. In Eurasia it is found from Scotland and southern Fennoscandia south to Morocco, Algeria, and the offshore Atlantic Islands, east through Lebanon, Afghanistan, and the Himalayan plateau to central China and Formosa, then north to northern Russia, southern Yakutsk, and Kamchatka. In North America it ranges from the Pacific Northwest through most of the Great Basin, the Rocky Mountains, and northern Sierra Nevada.

According to Donisthorpe (1927), *niger* probably occurs over the entire British Isles, with the possible exception of the northern Scottish islands. O'Rourke (1950) reports that it is common in sandy areas along the Irish coast but is found inland only in the southern half of the country. Holgersen (1944) states that it is common throughout southern Norway, occurring north to Ringebu in central Norway. Forsslund (1947) has found *niger* in Sweden as far north as Lima, Kopparberg. I have seen specimens from Ekenäs, Finland (O. Wellenius leg.; USNM), and Karawajew (1912) reports it as far north as Novgorod in European Russia.

Judging from the abundant material in collections lent to me, the vast number of records in the literature, and the past statements of many European authors, *niger* is very abundant throughout most of central and western Europe. Southward, it is still common in northern Spain from Catalonia to the Basque provinces (published records mostly by Santschi), and has been reported from near Madrid (Santschi, 1931), as well as Soure, in northern Portugal (Santschi, 1932). I have seen material from Centellas, Catalonia (de Xaxars leg.; MCZ); Algeciras, Cádiz (W. M. Wheeler leg.; MCZ); and the Alameda, Gibraltar (Wheeler leg.; MCZ). *Niger* is apparently common on Mallorca and Minorca in the Balearics (records by Eidmann

and Łomnicki; collections by Wheeler in the MCZ), and Łomnicki (1925) has recorded it from Santa Eulalia, Ibiza. According to Santschi (1931) this species has been taken in many localities through the middle and high Atlas ranges of Morocco, as well as Kenitra on the Moroccan coast. Verified records for Morocco, Algeria, and the offshore Atlantic Islands have already been given in the section on geographic variation.

Fig. 8. An outline of the known distributions of *L. niger* and *L. alienus* in North America.

Niger probably ranges throughout Italy. I have seen material from Bulach, Sardinia (A. H. Krausse leg.; USNM), and there are literature records for many of the adjacent Tyrrhenian Islands, including Sicily. Zimmermann (1934) gives many records for the Yugoslavian coast, noting that this species is scarce in southern Dalmatia. It is apparently rare in the Near East. I have seen series from the following localities in Lebanon: Hammana, 1100 meters; 2 km. south of Hermel, near the Orontes River, 600 meters; the mountain above the Kammouha Plain, 1900 meters, dealate queens (all K. Christiansen leg.; MCZ).

According to Karawajew (1926, 1927) *niger* has been taken in the Krimea and in many localities in the Caucasus. Kuznetzov-Ugamskij (1929b) found it common in the forests of northern Daghestan and sporadic in the drier southern area. Records verified for Afghanistan, Pakistan, and Soviet Central Asia have already been given in the sections on geographic variation and synonymy. Menozzi (1939) identified a form as "*emeryi*" collected at a number of localities in the Karakoram by the 1929 Duca di Spoleto expedition; this material, destroyed during the war, is probably true *niger* (see under synonymy). There is an excellent chance that *niger* occurs all the way across the southern face of the Himalayas at suitable elevations. Eidmann (1941), in his report on the ants collected by the Brooke Dolan expedition of 1934-35, lists a number of records from the eastern rim of the Tibetan Plateau and the adjacent Hsifan mountain country between 1800 and 3400 meters (localities include Yekundo, Tatsienlu, and Walingpin), and concludes that it is a common species through most of this area.

The following Chinese and Manchurian records have been made during the present revision: Beh Luh Din, Szechwan (D. C. Graham leg.; USNM); Hu Hsien and Miao T'ai Tze, Shensi (W. L. Brown leg.; MCZ); Soochow, Kiangsu (N. G. Gee leg.; MCZ); Nanking, Kiangsu (G. P. Jung leg.; MCZ); Peking, Hopeh (C. F. Wu leg.; MCZ); Tsinghua, Hopeh (Gee leg.; MCZ); Hishika, Manchuria (M. Tomiura leg.; Yasumatsu Coll.); Harbin, Manchuria (Y. Mori leg.; Yasumatsu Coll.). I have examined many series, principally in the Yasumatsu Collection, from over the entire Korean Peninsula; most of these were collected at random by school children, which suggests in itself that the species is abundant in the area. There is also a large

number of series in the Yasumatsu and Okamoto Collections and MCZ from Japan, principally from Kyushu, Shikoku, and Honshu, and *niger* must be widespread if not abundant there. It also occurs on the smaller surrounding islands, as shown by the following records (all Yasumatsu Coll.): Amboo, Yakushima (T. Shirozu leg.); Tomioka, Amakusa (Hori and Chô leg.); Tsutsu, Tsushima (Hori and Chô leg.). I have seen three series from Hokkaido (all Yasumatsu Coll.); Nishiashoro (R. Matsuda leg.); Ashoromura (Matsuda leg.); Nayoro (T. Takami leg.). Teranishi (1931) records it from the island of Shikotan, Kuriles. The Formosan records have already been given in the section on geographic variation.

Kuznetzov-Ugamskij (under synonymy) records this species from near Tashkent and Alma Ata, Soviet Central Asia. Holgersen (1943) records it from the Abakan Steppe, Khakass Autonomous Region, and from "Sistikem" (not located), Mongolia. Karawajew (1931) states that it has been found as far north in Siberia as the districts of Tobolsk, Tomsk, Yenisei, and Irkutsk, as well as the Akmolinsk region and Transbaikal. He examined a sizable collection from the remote Yakutsk District and obtained records ranging as far north as Ust-Kut on the Lena River in the west and the junction of the Aldan and Tympton rivers in the east. According to Karawajew also (1912, 1931), *niger* has been taken on Kamchatka and at Mauka and Chappusi on Sakhalin. Kuznetzov-Ugamskij (1929a) found it to be one of the commonest and most widespread ant species in the southern Ussuri region of the Soviet Maritime Territory.

The presence of this species in North America, living sympatrically with *sitkaensis* and *neoniger*, was discovered for the first time during the course of this revision. I have included below records of all of the series which have been examined. WASHINGTON: Blewitt Pass, Kittitas Co. (W. S. Creighton leg. and Coll.). OREGON: Willow Creek Campgrounds, Warner Mts., Lake Co. (B. Malkin leg. and Coll., MCZ). CALIFORNIA: Lake Tahoe (W. M. Wheeler leg.; MCZ). IDAHO: Double Springs Summit, Lost River Range (Creighton leg. and Coll.); Rock Creek Ranger Station, Twin Falls Co., 6400-6800 feet (Malkin leg. and Coll., MCZ); Bloomington Peak, Wasatch Range, Franklin Co., 8500-9000 feet (Malkin leg. and Coll., MCZ). MONTANA: Lake McGregor, Flathead Co. (Creighton

leg. and Coll.). COLORADO: Broadmoor, El Paso Co. (MCZ); Cascade, El Paso Co. (MCZ); Manitou Springs, El Paso Co. (W. M. Wheeler leg.; MCZ); Florissant, Teller Co. (2 series, T. D. A. Cockerell and W. M. Wheeler leg.; MCZ); Salida, Chaffee Co. (Wheeler leg.; MCZ). UTAH: Heber, Wasatch Co. (A. W. Grundmann leg.; Cole Coll.); Alta, Salt Lake Co. (Grundman leg.; Cole Coll.); Ogden, Weber Co. (G. F. Knowlton leg.; Cole Coll.); White Canyon, Natural Bridges National Monument, San Juan Co. (C. T. Brues leg.; MCZ). NEW MEXICO: 12 miles east of Taos, Taos Co., 7250 feet (A. C. Cole leg. and Coll.); Ute Park, Colfax Co., 7400 feet (Cole leg. and Coll.); Eagle Nest, Colfax Co., 2 series 8000 and 8600 feet (Cole leg. and Coll.); 2 miles south of Raton Pass, Colfax Co., 7700 feet (Cole leg. and Coll.); Capulin Mountain National Monument, Union Co., 7750 feet (Cole leg. and Coll.); Las Vegas, San Miguel Co., 6400 feet (Cockerell leg.; MCZ); Hayne's Canyon, Sacramento Mts., Otero Co., 8000 feet (Wheeler leg.; MCZ); Willow Creek Ranch, Mogollon Mts., Catron Co., 8300 feet (Cole leg. and Coll.).

ECOLOGY. Gösswald (1932) has presented a detailed and informative account of the habitat preferences and nesting habits of this species in Germany. He found it to be one of the most abundant and adaptable native ants. It occurs in deciduous, coniferous, and mixed forests, along forest borders, in hedgerows, and in open meadows; it thrives on cultivated land and occasionally enters houses. In forests it tends to nest in rotting tree trunks. In exposed situations with little vegetation cover, it nests mostly under stones. In meadows, along grass-grown paths and forest gardens, and in gardens, it frequently builds earthern mounds, especially where the soil is moist and the ground vegetation dense. Such mounds are irregular in shape and apparently designed to surmount the surrounding vegetation, with the result that they are often quite massive and may exceed 50 cm. in height. In a random field sample, Gösswald found 625 nests under stones, 350 in mounds, and 130 in rotting wood. The species is said to occasionally construct carton nests out of macerated plant material and humus, especially when it nests under stones in pine woods; the carton material closely resembles that characteristically manufactured by *L. fuliginosus.*

The North American population shows a similar latitude in

habitat preferences. Field notes supplied me with 16 collections by A. C. Cole and Borys Malkin seem to indicate a general preference for drier and more open situations. The majority of the 16 were taken in open forest of variable composition, while several were taken in meadows and grassy roadstrips. One was taken in a dry rabbitbrush association (*Chrysothamnus*) near Eagle Nest, N. Mex. (Cole, see under distribution). Another was taken near timberline in a zone of stunted fir (Bloomington Peak, Wasatch Mts., Idaho; Malkin). The Eagle Nest colony was found in soil at the base of a bush; all of the others were taken under stones.

The previously published Asiatic records seem to indicate broad adaptability also. The Yalung-Yangtse collections recorded by Eidmann (1941) were made both in moist river valleys and in the high grassland of the Tibetan Plateau. All were from under stones. Kuznetzov-Ugamskij (1929a) notes that in the Ussuri region this species occurs under the "widest environmental conditions."

Ecological data accompanying several peripheral collections determined during this revision are noteworthy. On the Canary Islands (Gran Canaria, Teneriffe, La Palma) Wheeler (1927) found *niger* mostly in moist, shady spots between 1500 and 5000 feet. At Las Mercedes, Teneriffe (2500 feet), it was the only ant species found in a forest of tree-heath (*Erica arborea*) and laurel (*Cerasus lusitanicus*). At Ponta Delgada in the Azores *niger* occurred abundantly with *Tetramorium caespitum*, nesting under stones and foraging over the ground in files. In Lebanon, Christiansen (*in litt.*) took workers under rocks in mesophytic forest at Hammana and dealate queens from rotting wood in spruce forest above the Kammuoha Plain. Workers were also taken with the aid of a Berlese funnel from around the roots of grass growing on the banks of the Orontes River two miles south of Hermel. This last locality is surrounded by scrub desert and is ten miles from the nearest well developed woodland, representing an extreme habitat record for *Lasius* in general and a very extraordinary one for *niger* in particular.

Niger has generalized food habits. Many authors have observed it gathering insect remains, floral nectar, and the honeydew (excreta) of Homoptera and larval Lycaenidae. Eidmann (1926) and others have suggested that the insect honeydew

makes up the bulk of the diet. According to Donisthorpe (1927), in a review of the food habits of this species, *niger* has been observed occasionally to gather seeds of such plants as *Viola, Galium,* and *Ranunculus;* Scott (1926) has seen it collecting seeds of *Chelidonium.* But apparently no one has checked to see if the seeds are actually used as food.

The pastoral habits of *niger* have been the subject of an excellent study by Eidmann (*ibid.*). Certain aphids overwinter in the nests of *niger* and are brought out and placed on the host plants in the spring. At first the aphids are returned to the shelter of the nests each evening. Later, as the nights grow warmer, the herds are left permanently in place. Certain of the workers function as guards (*Wächter*) during the day, remaining constantly at fixed posts; one worker was observed to return to the same spot each day for eight days. The workers appear to reduce predation by the braconid *Trioxys,* and on several occasions Eidmann saw them in the act of driving off workers of other ant species. Büsgen (1891) has observed *niger* workers combating chrysopid larvae in similar fashion. By counting the number of workers returning to the nest gorged with honeydew, Eidmann estimated that a large colony of *niger* may consume as much as a liter of this material in the course of a summer.

According to Eidmann, *niger* is principally nocturnal. Its above-ground activity, as measured by the number of ants soliciting honeydew, is highest at midnight and lowest in the early morning. The workers do all they can to avoid light; in order to work above ground they build turret-shaped shelters around the bases of aphid-infested plants and connect these with the nest by means of covered pathways.

Eidmann (1943) has included this species in a general study of overwintering in ants. Most of the workers of the colony move deep into the center of the nest, concentrating in a few chambers. A small number remain with the aphids in the special chambers where these insects are housed. Brood, in the form of small larvae, may be present or lacking.

According to Donisthorpe (1926), who has undertaken a thorough review of the European literature on the subject, the nuptial flights of *niger* take place in the afternoon and early evening from early July to mid-September. There are no records of nuptial flights in North America, but winged reproductives

have been taken *in nido* from July 3 (Sacramento Mts., N. Mex.) to September 1 (Alta, Utah). Stray males and queens, possibly engaged in a nuptial flight, were found at Heber, Utah, on September 7 (A. W. Grundmann). Eidmann (1926) has studied reproduction and nest-founding in this species in Germany. The pair copulate in flight, fall to the ground, and separate. The queen, without attempting to take flight again, soon drops her wings and seeks cover. The first eggs are laid the following spring, and the first adult brood hatches that summer. One queen was observed to go without food for 382 days in the normal course of founding a colony.

SYNONYMY. *Lasius niger* var. *alieno-niger* Forel. True hybrids between the European populations of *niger* and *alienus* must be very rare or non-existent. Taking into account the strong allometry shown by both species in the chief diagnostic character, I have failed to find a single European nest series which I could call an interspecific hybrid (Fig. 6). The series determined as *alieno-niger* in the MCZ (including the Finzi Collection) have invariably turned out to be small *niger* workers. But even if true hybrids were to be found eventually, and these included the *alieno-niger* types, the name definitely implies a special hybrid origin and cannot be used under the recent revisions of the International Rules of Zoological Nomenclature (Hemming, 1953).

Lasius niger flavescens Forel. Lectotype by present selection, a worker in the AMNH. Pronotum crushed on right side, HW 0.86 mm., SL 0.87, SI 101, seta count 37. This specimen has an unusual body coloration, a light yellowish brown of the shade typical of *L. umbratus*. It also has unusually abundant body hair, 27 standing hairs projecting beyond the thoracic border and 18 beyond the propodeal border when the alitrunk is seen in side view, but this is still within the extreme limits of normal *niger* variation. In suggesting synonymy in this case, I do not discount the remote possibility that *flavescens* may eventually be shown to represent a distinct Central Asian sibling of *niger*.

Lasius niger emeryi Ruzsky. The principal characters offered by Ruzsky are paler color (reddish yellow alitrunk) and short oblique hairs on the scapes and tibiae. The hairs are sparser on the scapes than on the tibiae and presumably overall sparser than in the typical *niger*. I believe that this form represents an

intermediate to the geographic variant already described as characterizing Formosa and ranging west to Pakistan. In fact, a specimen judged as such from Nathagali, N. W. F. P. (Weber Coll.), not far from the *emeryi* type locality, agrees well with Ruzsky's description except for a darker body coloration.

Kuznetzov-Ugamskij's *Acanthomyops niger nitidus, A. niger alienus* var. *pilicornis*, and *A. niger* var. *minimus* were described as trivial variants of *niger*. *Nitidus* was characterized as having a more shining sculpture and *pilicornis* as having scattered oblique hairs (see under geographic variation for this character), while *minimus* was distinguished only by smaller size. All three seem well within the normal variation of *niger*.

Lasius emarginatus var. *nigrescens* Stitz. Lectotype by present selection, a queen in the Berlin Museum. HW 1.51 mm., SL 1.28 mm., SI 85, ML 0.19 mm., thorax width anterior to tegulae 1.87 mm. Eight syntopotype queens from the same collection were also examined. The type series is typical *niger* in pilosity, color, and alitruncal profile. The SI is at the upper extreme obtained in measurements of ten series of *niger* from eastern Asia, but the ML is below the range of the same series (and of *emarginatus*) and well within the range of the European *niger*. There is no evidence that *emarginatus* occurs this far east.

Lasius niger coloratus Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.71 mm., HW 1.04 mm., SL 1.07 mm., SI 103, ML 0.20 mm., EW 0.20 mm. One other syntype worker examined. These two specimens are typical of the Formosan pilosity variant described in the section on geographic variation.

Lasius emarginatus var. *japonicus* Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.62 mm., HW 0.96 mm., SL 0.98 mm., SI 102, ML 0.20 mm., EW 0.19 mm., seta count 21. One other syntype worker examined. These specimens are typical *niger*, conforming to the general trend in the eastern Asiatic population by having appendage length in a zone intermediate between *niger* and *emarginatus*. The appendage pilosity seems to be somewhat diminished, but it is impossible to tell with certainty whether it fits the regression zone typifying northeastern Asia.

Lasius transylvanica Röszler. Prof. Röszler (*in litt.*) has informed me that the types of this specimen are at present un-

available to him and may have been destroyed during the Second World War. The species is supposed to be close to *niger*, differing by having hairless tibiae associated with normally hairy scapes. It is said to be peculiarly adapted to living in the vicinity of water on the floodplain of the Nyárad River and to show corresponding behavioral differences. It is my personal opinion that Röszler at the most was observing ordinary *niger* under exceptional ecological conditions and that the morphological characters may have been unduly exaggerated. I think the most practical course at the present time would be to place *transylvanica* in the provisional synonymy of *niger* to await the day that Röszler's observations can be repeated.

Lasius alienus (Foerster)
(Subg. *Lasius*)

Formica aliena Foerster, 1850, Hymenopterologische Studien (Ernst Ter Meer Publ., Aachen), **1**: 36–38; worker, male; original description. Type locality: Lousberg; a suburb of Aachen, Germany.

Prenolepis lasioides Emery, 1869, Ann. Accad. Natur. Napoli, **2**: 6–7; pl. 1, figs. 3, 3A; worker, queen, male; original description. Type locality: Naples, Italy. NEW SYNONYMY.

Lasius niger var. *lasioides*, Ruzsky, 1905, Formicariae Imperii Rossici, p. 310.

Formicina nigra lasioides, Emery, 1916, Bull. Soc. Ent. Ital., **47**: 177.

Lasius alienus lasioides. Zimmermann, 1934, Verh. Zool.-bot. Ges. Wien, **84**: 49.

Prenolepis fuscula Emery, 1869, Ann. Accad. Natur. Napoli, **2**: 8; worker; original description.

Lasius fumatus Emery, 1870, Bull. Soc. Ent. Ital., **2**: 194. *Nomen pro Prenolepis lasioides.*

Lasius niger alienus, Forel, 1874, Les Fourmis de la Suisse, p. 46.

Formica pallitarsus Provancher, 1881, Canadian Naturalist, **12**: 355–356. Synonymy by André, 1887, Revue d'Ent., p. 288.

Lasius niger var. *americanus* Emery, 1893, Zool. Jahrb. Syst., **7**: 639; worker, queen, male; original description. Type locality: Virginia, by present restriction. NEW SYNONYMY.

Lasius americanus, E. Gregg, 1945, Ann. Ent. Soc. Amer., **38**: 530.

Lasius alienus americanus, Creighton, 1950, Bull. Mus. Comp. Zool., **104**: 419.

Lasius niger var. *grandis* Forel, 1909, Ann. Soc. Ent. Belg., **53**: 104–105; worker; original description. Type locality: Ronda, Malaga, Spain. NEW SYNONYMY.

Lasius niger alienus var. *alieno-americanus* Wheeler, 1917, Proc. Amer. Acad. Arts Sci., Boston, **52**:*525–526; queen; original description. Type localitly: Banff, Alberta; by present restriction. NEW SYNONYMY.

Lasius niger turcicus Santschi, 1921, Bol. Soc. Esp. Hist. Nat., **21**: 115–116; worker, *nec* queen; original description. Type locality: Ankara, Turkey. NEW SYNONYMY.

Lasius niger lasioides var. *barbara* Santschi, 1921, ibid., p. 170; worker, original description. Type locality: Sidi Aïch, Tunisia. NEW SYNONYMY.

Lasius brunneus var. *barbara* Santschi, 1936, Bull. Soc. Sci. Nat. Maroc, **16**: 208.

Acanthomyops niger alienus var. *flavidus* Kuznetzov-Ugamskij, 1927, Rev. Russ. Ent., **21**: 189; worker; original description. Type locality: Dzhungarski Ala Tau Mountains, Alma Ata, Kazakh S. S. R., Soviet Central Asia. NEW SYNONYMY.

Acanthomyops niger alienus var. *turkmenus* Kuznetzov-Ugamskij, 1927, *ibid.*, p. 189; worker; original description. Type locality: Geok Tepe, Turkmen S. S. R., Soviet Central Asia. NEW SYNONYMY.

Lasius brunneus var. *obscurata* Stitz, 1930, Mitt. Zool. Mus. Berlin, **16**: 239–240; worker, queen; original description. Type locality: Dschailgan, Karateghin, western Pamirs, Tadzhik S. S. R., Soviet Central Asia, 1800 meters. NEW SYNONYMY.

Lasius alienus illyricus, Zimmermann, 1934, Verh. Zool.-bot. Ges. Wien., **84**: 50–52; worker, queen, male; original description. Type locality: Dubrovnik, Yugoslavia. NEW SYNONYMY.

Lasius alienus var. *pannonica* Röszler, 1942, Siebenbürgischer Ver. Naturw., Hermannstadt, Verh. und Mitt., **91-92**: 40; worker, queen; original description. Type locality: not designated. NEW SYNONYMY.

Lasius alienus var. *pontica* Stärcke, 1944, Ent. Ber., **11**: 156–157; worker; original description. Type locality: Neu Athos (Nowyi Afron), Caucasus, Georgian S. S. R. NEW SYNONYMY.

DIAGNOSIS. All three castes are extremely close to *niger*. The only character found to be of consistent diagnostic value is quantity of appendage pilosity, described in detail below.

Worker. Within the PW range of 0.53-0.70 mm., the seta count is always less than 20 and usually less than 10. The seta count is strongly allometric, making it advisable to determine individual specimens by comparing them with the regression zones of Figure 6. In Europe the regression zones of *niger* and *alienus* are parallel but well segregated; the *alienus* line is set so that the great majority of workers have seta counts of less than 5, while most *niger* exceed 20. In eastern Asia, on the

other hand, *alienus* evidently becomes scarcer, and the *niger* zone shifts down and forward to become contiguous with that of *alienus*. As a result, a small number of individuals cannot be safely determined to either species.

Queen. Seta count never exceeding 10 and usually 0.

Male. Seta count almost always 0.

TYPES. Dr. H. Bischoff has informed me that no syntypes of *alienus* can be located in the Foerster Collection in the Berlin Museum. What may be part of the type series has been found instead in the Mayr Collection and lent me by Dr. M. Beier. This consists of two pins, one holding two workers and the other a single male, labelled "Aach. Först/Las. alienus det. Mayr." The workers are identifiable as typical *alienus*.

FURTHER DESCRIPTION. *Worker*. Size ranging and averaging smaller than in *niger*. In a sample of 147, with no more than 2 per nest series, mean with standard error 0.56 ± 0.004 mm., standard deviation 0.054 mm. Color averaging lighter than *niger*, although total variation in both species shows complete overlap.

Queen. Size averaging smaller than *niger* when the North American populations are included.

Males. Size range about the same as in *niger* and showing parallel geographic variation. Mandibles typically of *niger* type, but in two series (Engadin, Switzerland, Kutter leg. and Coll.; Hornet, Beltrami Co., Minn., A. Achenbach leg., G. C. Wheeler Coll.) the mandible type is closer to the intermediate type already described for *L. brunneus*. Subgenital plate showing the same wide variation as in *niger*; series from Godinne, Belgium (A. Raignier leg.; MCZ) and the Engadin Valley, Switzerland (Kutter) encompass within themselves the full variation from the unilobed to bilobed condition.

GEOGRAPHIC VARIATION. Two significant independent trends have been noted in *alienus* and are described in detail below.

(1) The entire North American population appears to be separable as a unit from the Eurasian on the basis of male size (Fig. 7). Despite a strong partition between the two populations, it will be noted that both fall along the same HW-paramere length regression zone, and some overlap in individual measurements exists, so that the two populations cannot be

considered as distinct species on the basis of male size alone. No clinal trend within either population was noted. Correlated with this morphological character is a striking ecological difference, to be treated in some detail later. *Alienus* males from eastern Asia were not available during the present study.

(2) In the area encompassing the Balkans and northwestern Iran, appendages are often elongated as in the related species *emarginatus*. During the present study *alienus* with scape indices in the *emarginatus* regression zone (Fig. 5) have been recorded from the following localities: Dubrovnik, Yugoslavia (*illyricus* Zimmermann syntypes); Cetinje, Yugoslavia (Kutter Coll. and MCZ); Karlovo, Bulgaria (J. H. Kendall leg.; MCZ); Caspian, northwestern Iran (P. A. Buxton leg.; Oxford University Museum). An intermediate condition occurs in series from Lushnja, Albania (MCZ); Ankara, Turkey (*turcicus* Santschi syntypes); and Talysch District, Azerbaijan S. S. R. (MCZ). The character may also occur in Stärcke's var. *pontica* from Neu Athos, Georgian S. S. R. (see under synonymy). It may predominate in central and southern Yugoslavia, judging from the rather limited number of series examined from there, but it is less common or absent in adjacent areas. Numerous series from Bulgaria, Albania, the Istria-Cherso region, and northeast Italy, along with a few others from Greece, Lebanon, Turkey, Iraq, and Georgian S. S. R. all fit in the *alienus* regression zone. Farther east, a series from Srinigar, Kashmir (full citations for this and the following records are given in the next section) appears to fall between the *brunneus* and *alienus* zones, but the workers are too small to afford exact placement, since *brunneus* minimas of comparable size have not been available. A single worker from the Duany Tau Mountains, Kazakh S. S. R., falls in the upper *alienus* zone. The type series of Stitz's "*brunneus* var. *obscurata*", from the western Pamirs, falls in the middle of the *alienus* zone. Series from Kunming, China; Harbin, Manchuria, and Seoul, Korea, are well within the *alienus* zone. The entire North American population also falls within the *alienus* zone.

The appendage elongation trend in the Balkans is significant on two counts. First, *alienus* tends to converge toward *emarginatus* in the appendage character in the same area where *emarginatus* converges toward *alienus* in color. As a result, two of the important differences which separate these species over most of

their ranges are lost. Second, *alienus* copies in this area a trend taken by *niger* over much of its own range. But where *alienus* occurs in North Africa and eastern Asia, it does not follow *niger*, while *niger* in turn fails to follow it in the Balkans.

DISTRIBUTION (see also Fig. 8). *Alienus* has the widest distribution of all the members of the genus. In Eurasia it is found from the British Isles and southern Fennoscandia south to Morocco-Tunisia, east through Lebanon and Iraq to Kashmir and southern China, and north into European Russia, central Asia, China, and Japan. Unlike *niger*, it apparently does not occur in the Balearics, Canaries, and Azores, or in Formosa. In North America it is found from southern British Columbia to Nova Scotia and south to the mountains of Durango, Mexico, in the west, and to northern Florida in the east.

In England, according to Donisthorpe (1926), *alienus* is less common than *niger* and has been collected northward only to the central counties of Suffolk and Oxford. O'Rourke (1950) finds it scarce but widespread in Ireland. Stitz (in Strand, 1912) gives two records from southern Norway, but Holgersen (1944) in an extensive faunal study failed to find it in that country. I have seen two collections from southern Finland: Lappvik (O. Wellenius leg.; USNM), and Metsäpirti (Forsius leg.; MCZ). Ecological and local faunal studies by a number of European authorities indicate that *alienus* is subordinate to *niger* in most of northern and central Europe but is more prominent along the Mediterranean coast. It occurs sporadically through Spain, being recorded from the provinces of Catalonia and La Mancha by Menozzi (1932). I have verified the following two North African records: Biskra, Algeria (Stauder leg.; MCZ); Sidi Aïch, Tunisia (var. *barbara* Santschi syntypes). I have determined material from over most of Italy and a single series from Sorgono, Sardinia (A. H. Krausse leg.; MCZ). Several authors, particularly Emery (1915), have recorded it from the islands of Palmaria, Elba, Giglio, Asinara, and Sicily. I have seen series from many localities through Yugoslavia and Albania. It probably occurs over most of Greece; I have seen material from as far south as Andros Island, in the Cyclades (F. Werner leg.; MCZ). Forel (1911) records it from Athens, Menozzi (1928) records it from the Dodecanese, and Emery (1894) records it from Crete.

Since the Asiatic population is very hard to distinguish from the sympatric *niger* population and published records are manifestly unreliable, I have presented in the list below all records verified during the present study. Near East records are also included here for convenience.

TURKEY: Istanbul (K. Christiansen leg.; MCZ); Ankara (*turcicus* Santschi syntypes); Kars (C. Kosswig leg. and Coll., MCZ). LEBANON: mountain above the Kammouha Plain, 3 series at 1500 meters and 3 at 1800 meters (Christiansen leg.; MCZ). IRAQ: Shaglawa, near Ruwandiz (N. Weber leg. and Coll., MCZ). IRAN: northwest Iran, near the Caspian Sea (Buxton leg.; Oxford University Museum). U. S. S. R.: Krimea (W. Karawajew leg.; MCZ); Talysch District, Azerbajian S. S. R. (MCZ); Tiflis, Georgian S. S. R. (MCZ); Duany Tau Mountains, Kazakh S. S. R. (N. Kusnezov leg.; MCZ). KASHMIR: Srinigar (R. K. Enders leg.; Weber Coll. and MCZ). CHINA: Kunming, Yunnan Prov. (F. Silvestri leg.; MCZ). MANCHURIA: Harbin (Y. Mori leg.; Yasumatsu Coll.). JAPAN: Towada, Honshu (Esaki and Yasumatsu leg.; Yasumatsu Coll.).

For reasons already presented, literature records from Asia must be treated with extreme caution. I have noted the following which are of possible significance in extending the range as documented above: Ashkabad, Turkmen S. S. R. (Forel, 1903); Geok Tepe, Turkmen S. S. R. (var. *turkmenus* Kuznetzov-Ugamskij); southern Mongolia (Stitz, 1934). A record by Forel (1913) from Ceylon is of course highly dubious. The scarcity of records in the many Asian faunal lists published in the past tends to support my own conclusion that *alienus* is much less common there than *niger*.

In eastern North America, *alienus* is abundant from southeastern Canada to the southern Appalachians. The northernmost record known to me is Pleasantfield, Nova Scotia (W. H. Prest leg.; MCZ). I found the species abundant in Massachusetts and southern Ontario (Plantagenet, Ottawa, Sturgeon Falls, Deux Rivieres, Blind River), while large random collections by Mary Talbot in Livingston Co., Mich., and by Kenneth Kraft in Itasca State Park, Minn., establish the fact that it is generally abundant at this latitude. Collections by A. C. Cole and myself in the Appalachians of North Carolina and Tennessee show it

to be common there at intermediate elevations up to 5100 feet and ranging as high as 5800 feet (peak of Grandfather Mt., N. C.). It has been taken as far south as northern Florida, but is rare and locally distributed in the Gulf States. I have verified only the following records from this area.

GEORGIA: Mosquito Creek, Decatur Co. (P. B. Kannowski leg.; UMMZ and MCZ). FLORIDA: 6 miles south of Chattahoochee, Gadsen Co. (Kannowski leg.; UMMZ and MCZ); "Camp Torreya", Liberty Co. (T. H. Hubbell leg.; UMMZ); Monticello, Jefferson Co. (MCZ); Gainesville, Alachua Co., a single alate queen (MCZ). ALABAMA: Decatur, Morgan Co. (E. O. Wilson leg.; MCZ); Tuscaloosa (Wilson leg.; MCZ); Chunchula, Mobile Co. (Wilson leg.; MCZ); Phillipsville, Baldwin Co. (Wilson leg.; MCZ); Pollard, Escambia Co. (Wilson leg.; MCZ); Brewton, Escambia Co. (Wilson leg.; MCZ); Ariton, Dale Co. (Wilson leg.; MCZ); Blue Springs, Barbour Co. (Wilson leg.; MCZ); Chattahoochee State Park, Houston Co. (Wilson leg.; MCZ). MISSISSIPPI: no further data (USNM).

In the north-central states, *alienus* is abundant west to the limit of the deciduous forest. Judging from the exhaustive collections made by G. C. Wheeler and his students, it is one of the several dominant species of the genus in eastern North Dakota, but declines rapidly in the deciduous forest-grassland transition belt and is sporadic in the nearly treeless western half of the state. It is present but uncommon in the northern Rockies, being known only from the several following records. MONTANA: 2 miles east of Kiowa, Glacier Co. (E. O. Wilson leg.; MCZ); St. Marys, Glacier Co. (Wilson leg.; MCZ); Browning, Glacier Co. (W. S. Creighton leg. and Coll.); Fish Creek, Glacier Nat. Park (Creighton leg. and Coll.). IDAHO: North Fork, Lemhi Co. (Creighton leg. and Coll.).

Alienus must be sparse or absent in the southern Rockies and Great Basin; no records have been forthcoming from the large collections made there by Cole, Creighton, and Grundmann. It is widespread in the mountains of southern Arizona, as indicated by the following records: Rustler Park, Chiricahua Mts. (B. Malkin leg. and Coll., MCZ; and Creighton leg. and Coll.); Ramsey Canyon, Huachuca Mts. (Creighton leg. and Coll.); Stratton, Santa Catalina Mts. (W. M. Wheeler leg.; MCZ); Wet Canyon, Graham Mt. (Malkin leg. and Coll., MCZ). I have

seen one extraordinary collection from 32 miles west of El Salto, in the Sierra Madre Occidental of southern Durango, at 8700 feet (Creighton leg. and Coll., MCZ). There is an excellent possibility that the species is widely distributed at suitable elevations in other parts of northern Mexico.

Going northward along the Pacific coast, *alienus* has been encountered at Donomore Meadows in the Siskiyou Mountains of northern California, at 5600 feet (Creighton leg. and Coll.). North of this locality, it is apparently common through Oregon and Washington to southern British Columbia. OREGON: La Grande, Union Co. (Cole leg. and Coll.); Pistol River, Curry Co. (Malkin leg. and Coll., MCZ); Brookings, Curry Co. (Malkin leg. and Coll., MCZ); Portland (MCZ). WASHINGTON: Pullman (W. M. Mann leg.; MCZ); San Juan Island (T. Kincaid leg., Cole Coll.; Mann leg., MCZ). BRITISH COLUMBIA: Royal Oak, V. I. (MCZ); Lillooet (MCZ); Emerald Lake (W. M. Wheeler leg.; MCZ).

ECOLOGY. The Eurasian and North American populations differ markedly from one another in habitat preference. In North Africa and France (Bernard, 1950; Scherdlin, 1909), Ireland (O'Rourke, 1950), England (Diver, 1940), Germany (Gösswald, 1932), East Prussia (Skwarra, 1929), and Daghestan (Kuznetzov-Ugamskij, 1929), *alienus* typically inhabits open dry situations, nesting under stones and occasionally constructing crater entrances in open soil. It shows much less latitude in nesting sites than its sister species *niger*, but is more successful in cultivated areas. Bernard notes that in France it is able to replace *niger* entirely in pastures, even at high elevations, but tends to give way in turn to *Tapinoma simrothi* and *T. nigerrimum*. Diver, in an intensive study of the comparative ecology of *alienus* and *niger* in a local area in Dorset, found *alienus* restricted mostly to dry heath, whereas *niger* occurred in every major habitat studied. In Daghestan, Kutznezov-Ugamskij found *alienus* to have more southern affinities than *niger*. Where the two occur together, *alienus* is limited mostly to the steppes and mountain meadows (up to 11,000 feet), while *niger* occurs mostly in the forests.

In North America *alienus* reverses this habitat preference. Over its entire range on this continent, it shows a strong predilection for well shaded woodland, where it nests in rotting logs and

stumps and under stones. Among the hundreds of colonies I have encountered in the field in the eastern United States, nearly all conformed to this ecological character. It may happen, however, that at high elevations or at the northern periphery of its range, the species occasionally nests in open situations. At the summit of Grandfather Mountain in North Carolina, for instance, I found a small but vigorous population living under stones in an open blueberry-and-heath "bald". The elevation was 5800 feet, higher by 700 feet than any other collection of the genus made in the course of several field trips in the southern Appalachians.

I would like to venture the suggestion that the difference in habitat preferences between the Eurasian and North American populations may be a reflection of competition with various other members of the genus. In Eurasia *alienus* is replaced in most habitats, including woodland, by its extremely successful and abundant sister species *niger*. In North America it is replaced in nearly every available habitat except woodland by the equally successful and abundant members of the *neoniger* complex. As previously indicated in the description of the ecology of that species, *sitkaensis* occupies the same types of nesting sites as *alienus* and probably limits its northward spread. In general, one gains the impression that in Eurasia and North America *alienus* has been squeezed into relatively narrow ecological ranges by its congeneric competitors, but is nevertheless eminently successful within those ranges.

Alienus probably does not differ much from *niger* in food habits and ethology. Several Europeans, including Gösswald (*ibid.*) and O'Rourke (*ibid.*) have independently observed that *alienus* tends to be the more secretive of the two species. This is possibly correlated with the preference of this species in Eurasia for more exposed situations.

Records of nuptial flights in this species are too sparse to allow a rigorous comparison with *niger*. In Europe winged forms are found *in nido* during about the same period as for *niger*. I have records ranging from June (Trieste, MCZ; no further date) to October 28 (Italy, MCZ) without evident preponderance during any part of this period; a single pair were preserved in copula in October (Trieste; MCZ; no further date). In North America records range from May 30 (Decatur

Co., Ga.) to December 4 (Alachua Co., Fla.). Both of these are very exceptional dates, however; the majority of the other records fall in August.

SYNONYMY. *Prenolepis lasioides* Emery. Lectotype by present selection, a queen in the Mayr Collection. HW 1.43 mm., HL 1.26 mm., SL 1.10 mm., SI 77, seta count 0. One worker and one male syntype in the same collection also examined. Worker PW 0.38 mm., HW 0.57 mm., SL 0.67 mm., SI 123, seta count 0. Male HW 0.67 mm., paramere length 0.17 mm. With the possible exception of size and wing infuscation, the lectotype conforms precisely to *alienus* in every character. I have not seen other Palaearctic *alienus* this small but possess series from North America ranging to an even smaller size (e.g. Middlesex Fells, Mass.; W. L. Brown leg.; MCZ). The wings are more infuscated than usual but still within the range of normal variability of at least the North American population. The worker syntype is also exceptionally small, about the size of ordinary *alienus* nanitics, and does not differ from these nanitics in any character. Workers determined as *lasioides* by Forel (AMNH), Santschi (Santschi Coll.), and Finzi (MCZ) have also proven to be nothing more than small *alienus*. Differences quoted by various other authorities such as Zimmermann and Stärcke involve decrease of body hair and attenuation of body form, both purely allometric characters showing an even gradation from the largest workers of the "var. *grandis*" class to the smallest of the *lasioides* class. Finally, the male syntype is very small but otherwise a typical *alienus*.

Lasius niger var. *americanus* Emery. Lectotype by present selection, a worker in the Emery Collection labelled "Va. July 1, 85." PW 0.62 mm., HW 0.92 mm., SL 0.89 mm., SI 97, ML 0.17 mm., EW 0.18 mm., seta count 0. Two syntype workers and three syntype queens were also examined. All are typical *alienus*. As pointed out previously, the North American population can be separated as a unit from the Eurasian population on the basis of male size and will pass conventional subspecies requirements. My reasons for not employing trinomens in this and other such cases have already been explained in the introduction. If future myrmecologists for some reason choose to use this particular trinomen, however, they should bear in mind that Provancher's name *pallitarsus* has precedence, and *ameri-*

canus should be held in abeyance until its status as a *nomen conservandum* has been asserted (see "Principal of Conservation" in *Copenhagen Decisions on Zoological Nomenclature*, Hemming, 1953).

Lasius niger var. *grandis* Forel. Lectotype by present selection, a worker in the Forel Collection. PW 0.87 mm., HW 1.25 mm., SL 1.18 mm., SI 94, ML 0.21 mm., EW 0.24 mm., seta count 26. Syntype workers: PW 0.69 mm. and seta count 16; PW 0.69 mm. and seta count 19. The seta counts of these exceptionally large specimens place them in the *alienus* allometry regression zone; *niger* workers of comparable size have seta counts between 40 and 70. It is impossible to say whether *grandis* represents a geographic variant, since no other material from southern Spain has been forthcoming. North African series taken nearby are about average in size for the species.

Lasius niger alienus var. *alieno-americanus* Wheeler. This variety was created by Wheeler in a singularly haphazard way. In describing "*americanus*" from western North America, he actually had before him four species, *alienus* (Foerster), *crypticus* Wilson, *sitiens* Wilson, and *sitkaensis* Pergande. He noted that some of the queens in this material had longer wings and, erroneously assuming this to be a character of the European *alienus*, proposed his intermediate varietal name for them. Since he failed to designate types, there is no way to tell exactly which of the series of "*americanus*" he had in mind. I have designated the Banff, Alberta, series of *alienus* as a ceremonial procedure to formally dispose of the name. This series is typical for the species in every respect, while the males are of the size characteristic of the North American population.

Lasius niger turcicus Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.53 mm., HW 0.76 mm., SL 0.80 mm., SI 105, ML 0.16 mm., EW 0.17 mm., seta count 0. The single syntype queen was also examined. The lectotype is typical *alienus* in every character except for the geographic appendage character discussed previously and a more abundant body pilosity: seen in full face, two standing hairs extend beyond the right genal margin, and three beyond the left margin (typical *alienus* has, at most, one to a side). That this slight pilosity difference is not of species significance is suggested by the fact that a single series from Kammouha,

Lebanon (Christiansen) shows completely linking variation; and that it does not have special geographic significance is indicated by the fact that a series from Kars, Turkey (Kosswig) has a typical *alienus* pilosity. Apparently the main reason Santschi described *turcicus* was that he considered the syntype queen, supposedly associated with the lectotype worker, to be markedly different in proportion-characters from the typical *Lasius niger*. I am forced to agree with him fully, since the queen upon examination has proven to be not a *Lasius* at all, but *Prenolepis nitens* Mayr.

Lasius niger lasioides var. *barbara* Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.53 mm., HW 0.81 mm., SL 0.78 mm., SI 96, ML 0.15 mm., EW 0.18 mm., seta count 0. Three syntype workers also examined. That Santschi was able casually to jumble "*lasioides*" (=*alienus*) and *niger* together to form a mount for *barbara* and later to place this form under *brunneus* is both a fair indication of how little he knew about the genus in which he was prolifically describing new forms, and an illustration of the inane nomenclatural arrangements so often employed as a matter of course in ant taxonomy. The *barbara* types are somewhat darker and shinier than the average European *alienus*, but well within the range of normal variation of the species.

Kuznetzov-Ugamskij's *Acanthomyops niger alienus* var. *flavidus* and *A. niger alienus* var. *turkmenus* were described as nothing more than color and pubescence varieties of *alienus*. Both are evidently well within the range of normal variation of the species.

Lasius brunneus var. *obscurata* Stitz. Lectotype by present selection, a worker in the Berlin Museum. PW 0.59 mm., HW 0.90 mm., SL 0.92 mm., SI 102, ML 0.18 mm., EW 0.19 mm., seta count 0. Four syntype workers and the syntype queen also examined. The queen SI is unusually high (SI 80; HW 1.61 mm.), and both castes have unusually sparse body pilosity. Otherwise the series is typical *alienus*.

Lasius alienus illyricus Zimmermann. Lectotype by present selection, a worker in the MCZ from a series labelled "no. 532, Ragusa = Dubrovnik, Mte. Petka, Erdnest, Mai 1928, in Alkohol." PW 0.57 mm., HW 0.84 mm., SL 0.93 mm., SI 110, ML 0.20 mm., EW 0.19 mm., seta count 3. Ten other synnidotype

workers examined. This series is typical of *alienus* except for elongated appendages (see under geographic variation). The character in tibial pilosity emphasized by Zimmermann is not sufficient to distinguish this series from the European population.

Lasius alienus var. *pannonica* Röszler. The original description of the worker (*fide* Stärcke, 1944) contains practically nothing of diagnostic value. The queen, on the other hand, is stated to be smaller, more slender, and completely lacking pilosity. Since the whereabouts of the types are unknown (Röszler, *in litt.*), synonymy in this case is only conjectural and based on the assumption that the workers do not differ in actuality from typical *alienus*. There is an excellent possibility that the queen belongs to another formicine or dolichoderine genus.

Lasius alienus var. *pontica* Stärcke. The principal diagnostic character given for the type series, chosen from the type series of *alieno-brunneus* Forel after a lectotype for that variety had been selected, is the greater length of the scapes. This seems to be consistent with the trend already noted (under geographic variation) for the Balkans-Iranian population, and of which Zimmermann's prior form *illyricus* is a good example. Other characters in color, head shape, etc., given to distinguish *pontica* do not appear to be of taxonomic consequence when variation in the entire European population is taken into account.

Lasius emarginatus (Olivier)

(Subg. *Lasius*)

Formica emarginata Olivier, 1791, Encycl. Method. Insect., **6**: 494; queen; original description.

Lasius emarginatus, Mayr, 1861, Die europäischen Formiciden (Carl. Gerold's Sohn), p. 49.

Lasius niger emarginatus, Forel, 1874, Les fourmis de la Suisse (Nouv. Mem. Soc. Helv. Sci. Nat.), p. 46.

Lasius niger nigro-emarginatus Forel, 1874, *ibid.*, pp. 47, 49; worker, female; original description. Type locality: Switzerland. NEW SYNONYMY.

Lasius niger brunneo-emarginatus Forel, 1874, *ibid.*, p. 47; worker; original description. Type locality: Switzerland. NEW SYNONYMY.

Lasius niger emarginatus var. *brunneoïdes* Forel, 1874, *ibid.*, p. 47. NEW SYNONYMY (objective synonym of *brunneo-emarginatus* Forel).

DIAGNOSIS. As a member of the close-knit and difficult *niger* complex, *emarginatus,* like *niger,* must be determined by careful examination of multiple characters. It is easily separable from *niger* and *alienus* over part of its range on the basis of color and appendage length, but the three species tend to show convergent variation in the Balkans area, Mediterranean perimeter, and southcentral and eastern Asia.

Worker. (1) Scape and other appendages longer relative to body size than in all other members of the genus except *productus* Wilson. Eliminating the largest workers (HW 1.10 mm. or greater), the SI exceeds 103 in more than 95 per cent of nest series examined (Fig. 5); 95 per cent or more of *niger* and *alienus* in the same size range have an SI of less than 103, with the following exceptions: *niger* from the Balearics, North Africa, Canaries, and eastern Asia; and *alienus* from the Balkans and eastern Asia.

(2) As a corollary of (1), ML exceeding EW.

(3) Thoracic dorsum low and flattened with respect to the propodeum; if the heights of the propodeum and mesonotum are measured in profile from a base line drawn from the lowest point of the prosternum (anterior to the coxal insertion) to the lowest point of the mesosternum, the propodeum is *usually* about 1.05 $\times$ higher than the mesonotum; the two points are usually of equal height in *niger* and *alienus.*

(4) Scape with abundant standing hairs predominantly or entirely subdecumbent and tending to be concentrated on the distal third (Pl. 1, Fig. 8). Rarely the standing hairs may be predominantly suberect-erect or altogether lacking (see under further description below). *Niger,* especially from eastern Asia, occasionally approaches this typical *emarginatus* condition.

(5) Coloration of medium and large workers (i.e. workers with PW about 0.53 mm. or greater) usually distinctive. Alitrunk and petiole yellowish red, contrasting with both the head, which is medium to dark brownish red, and the gaster, which is dark brownish red. The alitrunk and petiole occasionally darken to approach the *niger-alienus* coloration; this divergent condition appears to preponderate in the Balkans population.

Queen. (1) Within a HW range of 1.61-1.70 mm. in a limited number of series measured, SI ranged 76-86. If this is a general condition it allows a 90 per cent separation from sympatric series

of *niger,* exclusive of the southern European and North African populations previously described.

(2) ML in this sample ranged 0.23-0.26 mm.

(3) Scape densely clothed with preponderantly subdecumbent and occasional decumbent hairs one-third to one-half as long as the maximum scape width.

(4) Alitrunk medium reddish brown, the head and gaster somewhat darker and tending to contrast against the alitrunk, but never so much as in the worker. This same coloration is closely approached by callow *niger* queens, so that separation on this character alone is difficult.

Male. (1) Within a HW range of 0.92-1.07 mm. in a limited number of series measured, SI ranged 70-76.

(2) ML in this sample ranged 0.24-0.28 mm.

(3) Scape with numerous decumbent hairs one-fourth to one-half as long as the maximum scape width, and few or no suberect or erect hairs.

(4) Subgenital plate typically similar in outline to that of *L. sitkaensis,* but larger (in five nest series measured, maximum transverse length ranged 0.59-0.73 mm.), and more arc-shaped: the posterior border tends to be evenly concave, sweeping back evenly to the prominent posterolateral flanges, while the anterior border is correspondingly convex (one exception noted, see further description below).

FURTHER DESCRIPTION. *Worker.* In a sample of 75, with no more than 2 per nest series, PW range 0.48-0.78 mm., mean with standard error 0.633 ± 0.006 mm., standard deviation 0.050 mm. Total range of SI 103-122, a strongly allometric character with highest values in the minimas. Head tends to be narrower than in *niger* and *alienus*, but considerable overlap occurs; in a limited series with HW range of 0.94-1.05 mm., CI varied between 84 and 91. Mandibular dentition similar to *niger*, with three or four basal teeth present, but differing statistically in two ways; (1) the four-toothed condition is more common, (2) the second tooth from the basal margin is often bifurcate, a condition rare in *niger*. Forty individuals each representing a different nest series were examined especially for dentition: 16 had three whole basal teeth, 16 had four whole basal teeth, and 8 had a bifurcate second tooth in a set of three. This variation is not allometric, since minimas may have four basal teeth,

and it does not appear to have a rigid genetic control, since two adjacent conditions can occur in the same nest series and even on different mandibles of the same individual. The petiole is less variable in outline than in other species of the complex; in all series examined the dorsal margin was shallowly and angularly impressed.

Scape pilosity as described in the diagnosis with the following three exceptions: a series from Dalmatia (H. Kutter leg.; Oxford University Museum) has a preponderance of suberect-erect hairs along the plane of the seta count; two series from Lebanon (Kammouha Plain and Wadi Jahhnam; K. Christiansen leg.; MCZ) lack standing hairs altogether.

Queen. Several interesting character trends have been noted which are, however, of less than diagnostic value. The scutum in profile tends to be more flattened than in other members of the subgenus. The posterior 5/6 of the scutum may be perfectly flat, whereas in *niger* the anterior third or more is usually involved in the anterior declivity. The posterior scutal border (transscutal suture) was found to be markedly sinuate in five out of six specimens examined; in *niger* and other *Lasius s. s.* this border is rarely more than feebly sinuate and often perfectly straight. The punctures of the scutum tend to be deeper and more distinctive in *emarginatus* than in *niger* and *alienus*.

Male. Paramere length 0.24-0.27 mm. in all series examined, apparently varying allometrically with respect to head width to about the same degree as in *niger*. In the total of eight specimens (5 localities) examined for genitalic characters, the setiferous lobes of the subgenital plate showed the same amount and kind of variation as in *niger* (*q.v.*). Two males from the same nest series (Lausanne, Switzerland; M. Bibikoff leg. and Coll.) encompassed the total possible variation, one with a single lobe and the other with two lateral lobes. Seven of the specimens showed the diagnostic outline previously described; one from Milan (USNM) was subquadrate and indistinguishable from *sitkaensis* except in size.

GEOGRAPHIC VARIATION. The alitrunk and petiole color of the worker occasionally deviates from the yellowish red typical of *emarginatus* by deepening to light or medium brownish red, so that the entire body becomes nearly as concolorous as in *niger* and *alienus*. This character may predominate in the Balkans (ex-

clusive of the Trieste area) since all four series I have seen from there possess it: Sofiya, Bulgaria (MCZ); Dalmatia (H. Kutter leg. and Coll.); S. Andrea Is., Dalmatia (Cori leg.; MCZ); Mali Daiti, Albania (MCZ). An intermediate condition, in which the alitrunk and petiole show a lesser degree of infuscation, occurs commonly in eastern Italy and northwestern Yugoslavia (see also under section on distribution): Momiamo, Istria; Cherso; Opcina and Lippizza, near Trieste; San Croce, Venezia Tridentina (all series in MCZ). The typical *emarginatus* coloration has been observed in series from the same localities in two cases, Cherso and Lippizza. It is also noteworthy that material from localities to the south and east of the Balkans (Lebanon, northwestern Iran, Krimea) possess the typical coloration.

There are vague indications of geographic variation in two other characters besides color. The single Krimean series contained the largest workers studied. Two series from Lebanon were the only ones in which standing hairs were completely lacking; suberect and erect hairs attained a maximum relative abundance in the single series from Iran.

DISTRIBUTION. This species appears to be limited to southern Europe and southwestern Asia. Balkan records other than those from northwestern Yugoslavia have already been fully stated in the preceding section. Below are given additional records which have been verified during the course of this revision.

FRANCE: Domfront (E. Lebis leg.; MCZ). SWITZERLAND: Lausanne (M. Bibikoff leg. and Coll.); Yvorne (W. M. Wheeler leg.; MCZ); Monte Generoso (Wheeler leg.; MCZ). AUSTRIA: no further data (G. Mayr leg.; MCZ). CZECHOSLOVAKIA: Kroměříz (O. Fiala leg.; MCZ). ITALY: Cremona, Lombardia (MCZ); Milan (USNM); Parma, Emilia (MCZ); Monte Faito, Sorrento, Campania (MCZ); Venice (Wheeler leg.; MCZ); Lucinico, Venezia Euganea (MCZ); Montello, Venezia Euganea (Ravasini leg.; MCZ); San Croce, Venezia Tridentina (B. Finzi leg.; MCZ); Duino, Divaccia, Lippizza, Opcina, and San Daniele, all near Trieste (Finzi leg.; MCZ); Monte Capanne, Elba, 600 meters (Moczarski-Scheerpeltz leg.; MCZ); Sicily, no further data (Kutter Coll.). YUGOSLAVIA (northwestern): Abbazia, Istria (Kutter leg. and Coll.); Momiamo, Istria (MCZ); Monte Taiano, Istria (B. Finzi

leg.; MCZ); Cherso (Ravasini leg.; MCZ). LEBANON: mountain above Kammouha Plain, 1900 meters; Wadi Jahhnam, N. W. Tripoli Prov., 700-1100 meters; Berouk Cedars (all three collections K. Christiansen leg.; MCZ). IRAN: northwestern Iran (Buxton leg.; Oxford University Museum). U. S. S. R.: "Utshan-su" (not located), Krimea (W. Karawajew leg.; MCZ).

Peripheral literature records, which must be taken with great reservation, include Oporto, Portugal (Stitz, 1916; Cephalonia, Ionian Islands (Emery, 1901); and Transcaucasia (Karawajew, 1926). So far as I know no one has claimed to have found this species in North Africa. Wheeler (1927) records "*nigro-emarginatus*" from Teneriffe, Canary Islands, but I have found no material so labelled in his collection.

Goetsch (1937), who has studied the biology of *emarginatus* in detail and seems to have great familiarity with it in the field, states that it is abundant in southern Italy, exceeding *niger* there, but diminishes rapidly toward the north. It is still common in the Italian Alps and Switzerland, ranging up to an elevation of 600 meters. It is very rare and sporadic in southern Germany, being limited to a few warm, dry areas such as the Würzburg Basin, part of upper Silesia, and sections of the Rhine and Neckar valleys.

ECOLOGY. This species nests mostly under rocks in open, dry situations. In Germany Gösswald (1932) found it in orchards, along forest borders, and in wasteland, nesting almost exclusively under rocks and in the crevices of rock walls, and avoiding woodland and moist situations in general. Nowotny (1931) found it uncommon in southwestern Poland, inhabiting dry areas under rocks and in walls. It was found in the same general type of habitat by Scherdlin (1909) in Alsace, by Donisthorpe (1928) in Italy, by Zimmermann (1934) in Yugoslavia, and by Goetsch (1937) in Italy, Switzerland, and Germany. Zimmermann found one colony in the wood of a pine stump on Campo Marzio in the Quarnerian Islands. Gösswald and Goetsch both report that the species occasionally enters houses.

Ecological data accompanying the Lebanon series previously mentioned are of interest because of the peripheral origin of these series (see under distribution). Dr. Christiansen collected the Wadi Jahhnam workers in a valley bottom well shaded by

mixed conifers and maples. The ants were foraging above ground along a stream bank. The Kammouha Plain workers were taken well up on a mountainside (1900 meters) under rocks in spruce woods.

Food habits, pastoral activities, and colony founding in this species have been treated briefly by Goetsch (1937). They do not appear to differ fundamentally from those already described for *L. niger* and are not worth bringing into the discussion here.

SYNONYMY. Although I have not seen types of Forel's two "intermediate" varieties *nigro-emarginata* and *brunneo-emarginatus,* the original description indicates that they are no more than insignificant color variants of *emarginatus. Nigro-emarginatus* was characterized by nothing more than a darker alitrunk color (see under geographic variation) and *brunneo-emarginatus* by a lighter alitrunk color and sparser pilosity. Both appear to be well within the normal range of variation for the species.

Lasius productus Wilson, new species
(Subg. *Lasius*)

DIAGNOSIS. A Japanese species closely related to *L. emarginatus,* but differing in all three castes by the possession of extraordinarily long appendages.

Worker. Within the HW range 0.86-1.12 mm., the SI is between 112 and 124 (see Fig. 5), and the ML exceeds the EW by about 1.3 $\times$.

Queen. ML in three queens examined ranging 0.32-0.34 mm., exceeding all other members of the genus.

Male. SI of the one specimen measured was 105, greatly exceeding all other members of the genus.

HOLOTYPE. A worker from Mt. Imano (Imanoyama), Shikoku (H. Okamoto leg. and Coll.). PW 0.72 mm., HW 1.04 mm., HL 1.17 mm., SL 1.23 mm., SI 119, ML 0.30 mm., EW 0.22 mm. Paranidotypes in the Yasumatsu Coll., MCZ, USNM, and Holgersen Coll.

FURTHER DESCRIPTION. *Worker.* Size averaging larger than in other members of the subgenus; PW 0.59-0.73 mm., mean 0.686 mm., based on 15 workers from 6 nest series. Anterior border of median clypeal lobe broadly rounded as in other *niger* complex members. Dentition very constant, with three perfectly

formed basal teeth in every specimen examined. Propodeum elevated relative to thorax as in *emarginatus*. Scapes densely covered with predominantly decumbent hairs; standing hairs very scarce or absent. Tibiae with sparser hairs which are mostly appressed. Color varying from concolorous medium brown as in *niger* (e.g. paratypes from Hikosan VIII-6-1940 and Sobosan IX-8-1933) to bicolorous with contrasting reddish brown alitrunk and dark brown gaster and head (e.g. paratypes from Hikosan XI-21-1939). The holotype nest series falls about intermediate between these two extremes; the holotype can best be described as having a medium reddish brown alitrunk barely contrasting with the gaster. None of the material examined reaches the extreme bicolorous condition of the typical European *emarginatus;* moreover, in *productus* the head is usually noticeably lighter than the gaster.

Queen. Characterized by its higher SI and tendency toward larger size. Following are measurements for three queens identified in the course of the present study. Japan, no further data (H. Sauter leg.; MCZ), HW 1.88 mm., SL 1.58 mm., SI 84, ML 0.32 mm.; Hikosan, Kyushu, IX-18-1939 (K. Yasumatsu leg. and Coll.), HW 1.79 mm., SL 1.55 mm., SI 87, ML 0.32 mm.; Hirooka, Shikoku VIII-29-1935 (H. Okamoto leg. and Coll.), HW 1.82 mm., SL 1.52 mm., SI 84, ML 0.34 mm.

Male. In the single specimen examined (Sobosan, Kyushu, IX-10-1933; Yasumatsu leg. and Coll.), HW 0.98 mm., SL 1.03 mm., SI 105. Subgenital plate very similar to that typifying *emarginatus*. Scapes densely covered with rather short, predominantly subdecumbent hairs. Tibiae with sparse, appressed to decumbent hairs.

DISTRIBUTION. Following are all of the records of the new species accumulated during the present study. KYUSHU: Hikosan (3 series; Yasumatsu, Esaki, and Nomura leg.; Yasumatsu Coll. and MCZ); Inugatake (Hori, Kawahara, and Yasumatsu leg.; Yasumatsu Coll. and MCZ); Sobosan (Yasumatsu leg. and Coll.); Sefuriyama (Yasumatsu leg. and Coll.). SHIKOKU: Imanoyama (holotype nest series); Hirooka, winged queen (Okamoto leg. and Coll.). HONSHU: Arima, near Kobe (M. Azuma leg.; USNM). TSUSHIMA: Isuhara-Sasutôge (Shirôzu leg.; Yasumatsu Coll.).

LASIUS NEONIGER Emery
(Subg. *Lasius*)

Lasius niger var. *neoniger* Emery, 1893, Zool. Jahrb. Syst, **7:** 639; worker; original description. Type locality: Virginia; by present restriction.
Lasius neoniger, Wheeler, 1910, Psyche, **17:** 83.
Lasius neoniger, E. Gregg, 1945, Ann. Ent. Soc. Amer., **38:** 534.
Lasius niger neoniger, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 420, part.

DIAGNOSIS. *Worker and queen.* Possessing the first two of the following characters in common with the other two members of the "*neoniger* complex" (*crypticus* Wilson and *sitiens* Wilson) and differing from these two species by the possession of the third.

(1) At least 20 per cent and often more than 90 per cent, of the nest series with the median of three basal teeth reduced in size relative to the two flanking teeth (see Pl. 1, fig. 3); in individuals where this tooth is absent, the space between the two remaining teeth is typically irregular in size and shape and usually larger in area than the basal-most tooth.

(2) The anterior border of the median clypeal lobe, when viewed in perfect full face (attaining maximum head length) and with the mandibles open, is obtusely angulate, the lateral faces straight and often meeting centrally to form a distinct angle (see Pl. 1, fig. 3); opposed to the broadly convex or parabolic condition of the "*niger* complex."

(3) Scapes and fore tibiae with abundant hairs, many of which are standing. The density declines allometrically, and nanitic workers (with PW about 0.40 mm.) may have seta counts of 0.

Male. Very similar to small individuals of *L. niger* except that the anterior border of the median clypeal lobe tends to be angulate as in the worker and queen. In the male this character is highly variable, however, and not all isolated individuals can be determined to species with certainty.

LECTOTYPE. By present selection, a worker in the Emery Collection labelled "Va.". PW 0.49 mm., HW 0.75 mm., SL 0.73 mm., SI 97, seta count 16. Typical for the species in dentition, clypeus, pilosity, and color.

FURTHER DESCRIPTION. *Worker.* PW 0.39 mm. (incipient colony) to 0.64 mm.; the range and dispersion are apparently

about the same as for *alienus* (*q. v.*). SI of series of average-sized to large workers falling in the *niger-alienus* regression zone, although two nanitics measured (Sudbury, Mass. incipient colony; Wilson leg.; MCZ) fell lower, just above the extrapolated *brunneus* zone — SL/HW ratios were 0.59/0.57 mm. and 0.59/0.58 mm. respectively. A similar dip in the regression zone has been observed in the sibling species *L. crypticus,* while the third member of the *neoniger* complex, *L. sitiens*, falls along the extrapolated *brunneus* zone. This indicates that the *neoniger* complex differs generally from the *niger* complex by having steeper regression zones. In body form, head shape, petiolar variation, etc., *neoniger* closely resembles *niger* and *alienus.* Appendage pilosity sparser and averaging shorter than in *niger*, with more hairs inclining to decumbent-subdecumbent, which condition occurs in *niger* in the Asiatic population only. Maximum color variation has been encountered within collections from the western U. S.: series from the White Sands National Monument, New Mexico, range to pale yellowish brown, with the head slightly darker than the remainder of the body; a series from Bishop, California, is a shade of dark brown about average for *niger* and *alienus.* The usual *neoniger* coloration is a light brown with feebly contrasting darker head.

Queen. Size range and dispersion apparently about the same as for *L. alienus.* The dentition and clypeal characters of the worker are repeated in this caste with exaggerated effect. The clypeus is typically very angular, contrasting with the evenly convex condition of the *niger* complex and the flat-to-emarginate condition of *sitkaensis.* A peculiarity of the dentition in this caste is the frequent occurrence of an offset basal tooth similar to that characterizing *sitkaensis;* but when this occurs, it is often present on one mandible only, it is usually larger and more acute than in *sitkaensis*, and it is rarely if ever accompanied by secondary teeth on the basal border. The wings are more opaque than in the *niger* complex but lack the pattern of basal infuscation characterizing *sitkaensis* and *brunneus.*

Male. HW 0.74-0.86 mm., dispersion apparently about the same as for the North American populations of *niger* and *alienus.* Genitalia size and configuration, including the posterior lobing of the subgenital plate, apparently the same as for these two species.

GEOGRAPHIC VARIATION. Series from the western United States, from Montana south to New Mexico and west to California, show the greatest total variability in size, color, and pilosity, but there is no definable unilateral trend in any single character. Four series taken in pure sand in the White Sands National Monument, New Mexico, are exceptionally hairy and light in color, both of which characters may represent adaptation

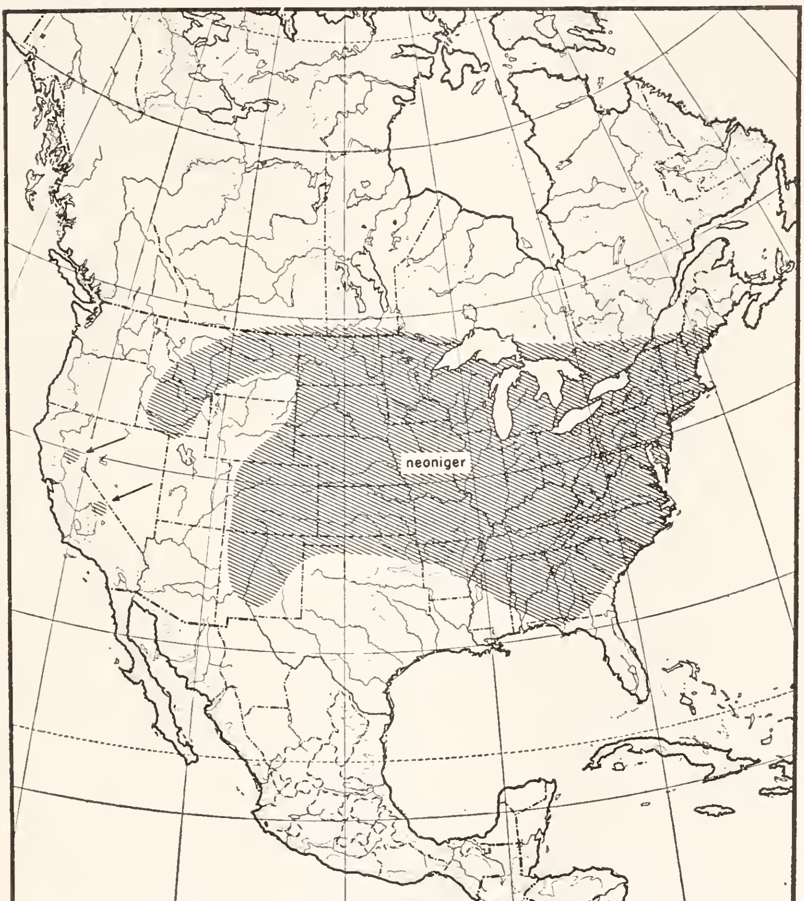


Fig. 9. An outline of the known distribution of *L. neoniger*.

on the part of the local population to the extreme environment at this locality.

DISTRIBUTION. (See also Fig. 9). *L. neoniger* is abundant in eastern North America and as far west as North Dakota and Iowa. West of the Great Plains it apparently diminishes rapidly; it is rather uncommon in the southern Rockies and is thus far completely unknown from the Pacific Northwest.

In the summer of 1952 I found it to be one of the dominant species of ants in a number of localities visited in southern Quebec and Ontario, including Montreal, Verdun, Lake Constance, Deux Rivieres, North Bay, Sturgeon Falls, and Blind River. Other southeastern Canadian records verified during the present study include Toronto (R. J. Crew leg.; MCZ) and Cloyne, Ont. (A. B. Klugh leg.; MCZ). There is no way of determining the northern limits of the species with available data.

Neoniger is one of the dominant ants in open habitats everywhere from New England to North Carolina and Tennessee. I found it extremely abundant in the vicinity of Washington, D. C., and Great Falls, Va., and at lower elevations in western North Carolina and eastern and central Tennessee. It maintains this abundance in the region of the Great Smoky and Black Mountains up to an elevation of about 5100 feet. At the latter elevation, on the southern slope of Mt. Mitchell, I found the species to drop off sharply, and so far as I know neither A. C. Cole, A. Van Pelt, nor I have ever collected it higher than this in the course of many field trips in the area.

The species has been taken in several localities in South Carolina (first four series in USNM): Batesburg, Lexington Co. (E. S. Titus leg.); Saluda Co.; Marion, Marion Co. (C. G. Ainslee leg.); Clemson College, Pickins Co. (M. R. Smith leg); Myrtle Beach State Park, Horry Co. (W. S. Creighton leg. and Coll.). It is rare in the Gulf States, being known only from the following several localities: Seeley's Pond, Seminole Co., Ga. (P. B. Kannowski leg.; UMMZ); Jackson Co., Fla. (Kannowski leg.; UMMZ); Tuscaloosa, Ala. (E. O. Wilson leg.; MCZ); Eufaula, Barbour Co., Ala. (Wilson leg.; MCZ).

Neoniger is abundant throughout North Dakota, as shown by the massive collections made by G. C. Wheeler and his students. I have seen material from South Dakota (Capa, Jones Co., MCZ; Brookings, H. C. Severin leg., MCZ), Nebraska (Grand Island,

R. P. Uhlmann leg., G. C. Wheeler Coll.; McCook, Redwillow Co., USNM; North Platte, Cole leg. and Coll.), and from various localities over Kansas (University of Kansas Coll., USNM, MCZ). I have seen a single series from Ware, Dallam Co., Texas (USNM), the only record of the genus from that state known to me.

Following are records from west of North Dakota and Texas which have been accumulated during the present study. MONTANA: Harlem, Blaine Co. (E. O. Wilson leg.; MCZ); Great Falls Air Base (Wilson leg.; MCZ). IDAHO: Hagerman, Gooding Co. (A. C. Cole leg. and Coll.); Twin Falls (Cole leg. and Coll.); Castleford, Twin Falls Co. (Cole leg. and Coll.). WYOMING: Guernsey, Platte Co. (USNM). COLORADO: Rist Canyon, Fort Collins (USNM); Denver (W. M. Wheeler leg.; MCZ); Salida, Chaffee Co. (Wheeler leg.; MCZ); Silverton, San Juan Co. (E. J. Oslar leg.; MCZ). NEW MEXICO: Albuquerque (L. D. Christenson leg., USNM; W. M. Wheeler leg., MCZ); White Sands National Monument, 4 series (Cole leg. and Coll.). CALIFORNIA: Bishop (Wilson leg.; MCZ); Yuba City (L. D. Christenson leg.; MCZ). There is an excellent possibility that the California records represent disjunct introduced populations, since they were both found in heavily populated areas.

There is in the United States National Museum a long uninidal series of *neoniger* labelled "Anchorage, Alas / 1947 / VIII-47 / F. R. DuChanois." I have contacted Lt. DuChanois and he assures me (*in litt.*) that this extraordinary record is to the best of his knowledge valid. He believes that the collection was made in the vicinity of the 18 milepost on the Anchorage-Fairbanks highway. "Most of the Formicidae were taken in pine-birch- (and occasionally hemlock) forested areas on the open ground . . . I am quite certain that the specimens did not represent transient incursions because of the relative remoteness of the ecological habitats in which they were taken." Nevertheless, the considerable range extension that this record represents for the genus, with the nearest specific record for *L. neoniger* in southern Idaho, makes it desirable to withold judgment until additional material can be secured.

ECOLOGY. This species nests almost exclusively in open areas, either under stones or in open soil in craters. In the eastern United States it is frequently the dominant ant in grassy

road strips, lawns, cultivated fields (cf. Talbot, 1953), and other disturbed situations. By virtue of this ruderal adaptation it has become one of the most abundant and conspicuous insects within its range. The only natural habitats in which I have found it dominant are prairie (North Dakota, Montana) and old beach dunes (New England coast, Great Lakes). It never penetrates deep forests and is scarce in open woods and well shaded forest borders.

One of the most interesting features of its ecological distribution is its clearcut microgeographic replacement by the woodland species *L. alienus.* The two species overlap to a limited extent in open, sunny woodland, where both may be found nesting under stones. But the bulk of the *neoniger* population occurs in completely exposed situations, in craters and under stones, while most of the *alienus* are in rotting stumps and logs in well shaded woodland. This replacement pattern can be developed into an intricate mosaic where the habitats are suitable. Such a situation is found at Ipswich Beach, Massachusetts, for example, where the two species occur together in a small stretch of littoral woodland covering about fifty acres. The woods at this locality consist principally of small trees of *Betula populifolia* (grey birch), *Prunus maritima* (beach plum), *Acer rubrum* (red maple), *Pinus rigida* (pitch pine), and several species of oak. They are dense in low swampy areas where they provide leaf litter and humus of varying thickness to the loose, sandy soil. They are broken at intervals however, by foot paths, animal trails, and sand ''blowouts''. The latter are shallow, barren depressions in the sand in which only scattered grass and *Hudsonia* shrubs grow. *L. neoniger* is limited to these open areas, its craters often occurring in dense concentrations where the sand is firmly packed and moist several inches below the surface. *L. alienus,* on the other hand, is entirely limited to rotting stumps, logs, and branches on the shaded forest floor. Under natural conditions there is probably always an ample supply of such nesting sites, since *Betula populifolia,* the dominant tree, is very short-lived, and dead trees must always be in abundance. The two species are thus sharply segregated ecologically, with the *neoniger* population consisting of a series of enclaves within a more or less continuous woodland *alienus* population. No instances of overlap were found; the closest approach was a colony of *alienus* in a rotting

log near the margin of a blowout and about seven feet from a cluster of *neoniger* craters.

Like other species of *Lasius*, *neoniger* is polyphagous, accepting both insect food and nectar. At Schroon Lake, N. Y. and Lake Constance, Ontario, I watched workers of this species foraging above ground in the early part of the night. The "trophophoric field" of the many nests observed did not seem to exceed two or three yards in radius, and the workers appeared to be engaged solely in gathering dead and crippled insects. A great variety of insects were accepted, including flies, leafhoppers, beetles, and spiders of various sizes. Using captive colonies maintained during a period of over a year, I have since learned that insects are readily accepted as food and are evidently necessary for successful colony growth.

The pastoral habits of this species have been dealt with in detail by S. A. Forbes' classic account (1894). He and later authors, including W. M. Wheeler, have referred to the species studied as "*americanus*" (treated herein as a synonym of *alienus*), but there can be little doubt, judging from the descriptions of the ecology, nesting habits, etc., as well as from a drawing later published by Forbes, that it was really *neoniger*. The mutualistic relationship between the *Lasius* and the cornroot aphid (*Aphis maidiradicus*) as explored by Forbes is very similar to that later demonstrated by Eidmann (1926) between the European *L. niger* and an epigaeic species of aphid. The ants gather the eggs of the fall sexual brood of the aphid, store them in the nests over the winter, and in the spring excavate special galleries by means of which they are able to place the newly hatched nymphs directly on the corn roots. When strange aphids are freshly presented to the ants above ground they are promptly carried into the nest and placed on the roots also.

Talbot (1946) has studied diurnation in this species. In ordinary summer weather the workers are mainly nocturnal. Activity begins to rise in late afternoon, continues through the night, and declines through the following morning. The species prefers cool temperatures (50°-60° F.) and high humidity.

Forbes (1908) and Tanquary (1913) have studied the life history of this species in some detail. Nuptial flights are recorded by them for the period September 5-October 18. Mr. B. D. Valentine (pers. commun.) has observed nuptial flights of this

species on Long Island, New York, during the first week of September over a period of several years. It has been my observation that flights occur mainly in September in the Boston area also. The earliest record for a flight is one which I observed at Bishop, California, on July 30, 1952. In so far as I know the flights always take place during the second half of the afternoon; the one at Bishop continued to dusk. In the collections available to me, I have found winged forms associated in the nest with workers from July 25 (Salida, Colo.) to October 13 (Denver, Colo.). Forbes and Tanquary both showed that colony founding in this species resembles that later described for *niger* and *flavus* by Eidmann (1931). The fecundated queens overwinter without brood and start laying eggs in the following spring.

Lasius crypticus Wilson, new species

(Subg. *Lasius*)

DIAGNOSIS. A western North American species very similar to *L. neoniger,* differing principally in the scarcity of hairs on the scapes and fore tibiae, and by the darker body coloration of the worker and queen. Linked to the "*neoniger* complex" by the possession of clypeal and dentition characters already detailed in the description of *neoniger*. Superficially resembles *alienus* and has been consistently determined as this species ("*americanus*") by past authors.

(1) In all three castes standing hairs are invariably absent on the scapes and fore tibiae along the plane of count (seta count, *q. v.*), while appressed decumbent hairs are rare or absent. These surfaces are covered only by a short, predominantly appressed pubescence.

(2) The worker and queen are almost invariably dark brown, rarely medium brown, opposed to the typically light brown coloration of *neoniger*. The males of the two species show broadly overlapping dark brown coloration.

(3) The worker has a proportionately shorter scape length than in *neoniger;* a small number of series of medium-sized to large workers, when measured, fell between the *alienus-niger* and *brunneus* SI-HW regression zones, while several nanitic series fell along the extrapolated *brunneus* zone. However, *crypticus*

and *neoniger* are too close to give this character diagnostic value by itself.

HOLOTYPE. A worker in the MCZ, selected from a large nest series collected four miles north of Gardar, Pembina Co., N. Dak., Aug. 31, 1949, with associated winged queens and males (E. L. Krause leg., acc. no. 138). PW 0.52 mm., HW 0.79 mm., SL 0.70 mm., SI 90, EL 0.19 mm., seta count 0. Fits the *neoniger* complex

Fig. 10. An outline of the known distributions of *L. crypticus* and *L. sitiens.*

in clypeus and dentition characters and is distinguished specifically by pilosity and color. Paranidotypes are in the MCZ, USNM, UMMZ, G. C. Wheeler Coll., Creighton Coll., and Cole Coll.

DISTRIBUTION. *Crypticus* has its center of abundance in the Great Plains of the western U. S. It apparently stops abruptly at the edge of the eastern deciduous forest, having never been collected east of the eastern tier of counties of North Dakota. It is relatively common in the Rocky Mountains and Great Basin, and reaches as far west as California and Oregon. In the following list are included all of the records accumulated during the present study. (See also Fig. 10.)

NORTH DAKOTA (all series in G. C. Wheeler Coll., except where otherwise noted; most with nest duplicates in MCZ): Pembina Co. (E. L. Krause leg., accession nos. 175, 178); Walsh Co. (W. E. LaBerge leg., acc. nos. 14, 15, 57, 91, 93, 94, 97, 99, 110, 117, 118, 119, 126, 132, 134, 233, 244, 251); Grand Forks Co. (J. N. Wheeler leg., acc. No. 9; L. Monda leg., acc. no. 901); Cass Co. (C. Schonberger leg., acc. nos. 5, 21, 34, 71, 141); Richland Co. (H. H. Osborn leg., acc. nos. 2, 23, 105, 133, 158, 159, 172, 183, 227); Ramsey Co. (UMMZ; P. B. Kannowski leg., acc. nos. 34, 51, 154, 176, 186, 326); McClean Co. (R. P. Uhlmann leg., acc. nos. 211, 216, 226, 256); Divide Co. (J. Davis leg., acc. nos. 8, 11, 12, 25, 50, 51, 57, 58, 66, 67, 76, 79, 82, 108, 110, 148, 149, 187, 188, 189, 190, 191, 192, 193, 194, 196, 198, 200, 209); Billings Co. (J. E. Goldsberry leg., acc. nos. 100, 150, 157); Golden Valley Co. (J. E. Goldsberry leg., acc. nos. 103, 105, 110); Stark Co. (R. P. Uhlmann leg., acc. no. 90); Slope Co. (Black Butte; E. and G. Wheeler leg.); Hettinger Co. (R. P. Uhlmann leg., acc. nos. 3, 6, 9, 23, 25). (While relatively common in several of the easternmost counties of North Dakota, *crypticus* was not present in a large collection of the genus made by Mr. Kenneth Kraft in Itasca State Park, Minnesota, nor has it been taken anywhere else in that state.) SOUTH DAKOTA: Capa, Jones Co. (MCZ); Hill City (T. Ulke leg.; MCZ). MONTANA: Culbertson, Roosevelt Co. (E. O. Wilson leg.; MCZ); Great Falls (Wilson leg.; MCZ). ALBERTA: Lethbridge (G. G. Hewitt leg.; MCZ). IDAHO: Hagerman, Gooding Co. (A. C. Cole leg. and Coll., MCZ); Twin Falls (2 series, Cole leg. and Coll., MCZ); Green Canyon Hot Springs, Madison Co. (B. Malkin leg. and Coll.,

MCZ); Donnelly and Cascade, Valley Co. (Wilson leg.; MCZ). WYOMING: Madison Junction, Yellowstone Nat. Pk. (Wilson leg.; MCZ); Dubois, Fremont Co. (W. S. Creighton leg. and Coll.). COLORADO: Boulder (W. M. Wheeler leg. and S. A. Rohwer leg., both MCZ; Creighton leg. and Coll.); South Boulder Canyon (T. D. A. Cockerell leg.; MCZ); Cheyenne Canyon, Colorado Springs (MCZ); Florissant, Teller Co. (Wheeler leg.; MCZ); Buena Vista, Chaffee Co. (Wheeler leg.; MCZ) Creede, Mineral Co. (S. J. Hunter leg.; MCZ). NEW MEXICO: Capulin Mt. Nat. Mon., Union Co., 7100 feet (Cole leg. and Coll., MCZ); 10 miles west of Cimarron, Colfax Co., 7100 feet (Cole leg. and Coll., MCZ); 16 miles east of Raton, Colfax Co., 6650 feet (Cole leg. and Coll., MCZ); 2 miles south of Raton Pass, 7700 feet (3 series, Cole leg. and Coll., MCZ); 11 miles north of Eagle Nest, in Taos Co., 9000 feet (Cole leg. and Coll. MCZ); 12 miles east of Taos, 7250 feet (2 series, Cole leg. and Coll., MCZ). UTAH: Henry Mts., Garfield Co. (Creighton leg. and Coll., MCZ); Long Valley Junction, Kane Co. (Wilson leg.; MCZ). CALIFORNIA: Hurkey Creek Camp Grounds, San Jacinto Mts. (Creighton leg. and Coll., MCZ). OREGON: Durkee, Baker Co. (B. Malkin leg. and Coll., MCZ).

ECOLOGY. The following generalizations are based on a few of my own observations along with field notes supplied me by G. C. Wheeler, A. C. Cole, and Borys Malkin. *Crypticus* is most abundant in prairies and tends to replace *neoniger* in the most dry, exposed situations. In eastern Montana and southern Idaho it was found thriving in a short-grass prairie-semidesert transition. At Cascade, Idaho, and in several localities in New Mexico, it was taken in open pine forest. At Green Canyon Hot Springs, Idaho, it was found in dry willow-poplar woods. In the great majority of cases it has been found nesting under stones, but occasionally (e.g. Donnelly and Cascade, Idaho) it constructs *neoniger*-like craters in open soil.

No nuptial flights of this species have been recorded. Winged reproductives have been taken with workers from July 9 (Great Falls, Mont.) to August 31 (holotype nest series, Pembina Co., N. Dak.). The majority of such records fall in the last half of July and first half of August. This would seem to be strong prima-facie evidence that the reproductive period of *crypticus* precedes that of *neoniger*.

LASIUS SITIENS Wilson, new species

(Subg. *Lasius*)

DIAGNOSIS. A small, light-colored species occurring in the southwestern United States and northern Mexico.

Worker. (1) The outstanding diagnostic character is the small eye size: maximum eye length (EL) only 0.21-0.25 $\times$ the HW, whereas it always exceeds 0.25 $\times$ the HW in *neoniger* and *crypticus* and members of the *niger* complex. The maximum ommatidium number in a line along the long axis of the eye is typically 11 in *sitiens,* and occasionally 10 or 12; in related species it is typically 14 or 15 and occasionally 13 or 16.

(2) Averaging smaller than other members of the subgenus; PW rarely exceeding 0.56 mm. and usually less than 0.54 mm.

(3) Scapes and tibiae lacking standing hairs.

(4) Color typically medium yellowish brown, rarely dark yellowish brown.

Queen. Very similar to the queen of *crypticus,* differing only in the following two characters.

(1) Averaging and ranging smaller; HW range in all available series 0.63-0.78 mm.

(2) Body medium to dark brown, with pale yellowish brown legs.

Male. In this caste the anterior border of the median lobe of the clypeus is broadly rounded, in contradistinction to the angular condition of the worker and queen of the same species, and males of *neoniger* and *crypticus.* Individuals are therefore not surely separable from small, faded *alienus* males. The following two characters represent distinctive trends but are not absolutely diagnostic.

(1) Averaging and ranging smaller than other members of the subgenus; HW range in all available series 0.63-0.78 mm.

(2) Body medium to dark brown, with pale yellowish brown legs.

HOLOTYPE. A worker in the MCZ, selected from a nest series collected 20 miles north of Flagstaff, Arizona, on U. S. Route 89, July 25, 1952, with associated winged queens and males (E. O. Wilson leg.). PW 0.50 mm., HW 0.71 mm., SL 0.68 mm., SI 95, EL 0.17 mm., 11 ommatidia counted along the long axis of the eye. Paranidotypes in MCZ, USNM, and Creighton Coll.

FURTHER DESCRIPTION. *Worker.* PW maximum range 0.40-0.56 mm. In a sample of 53 from as many nest series, mean with standard error 0.472 ± 0.006 mm., standard deviation 0.042 mm. Appendages noticeably shorter than in related species. Scape index low, falling along the extrapolated *brunneus* SI-HW regression zone, but overlapping the lower extremity of the *crypticus* zone. The funiculus is also shortened, to the extent that flagellar segments I and II are as broad as long or slightly (never more than 1.3 ×) broader than long, and segment III is as broad as long to slightly longer than broad; most of the range of this variation may be seen in single nest series. Maxillary palp segments V and VI subequal, quite short with respect to total body size, so that their length varies between 0.5 × and 0.8 × the maximum fore-tibia width. The head shape is slightly divergent from that of other species in that the largest workers show a "mature" allometric broadening of the head just behind the eyes; i.e. the allometric variation in head shape seen in larger species is expressed on a more diminutive scale in this species. Scapes and fore tibiae ordinarily devoid of hairs of any sort, although several decumbent to subdecumbent hairs were observed on the scapes in a single series from Sapello Canyon, New Mexico.

GEOGRAPHIC VARIATION. No trends were detected within the rather limited range of this species.

DISTRIBUTION. Below are listed all of the records of the new species accumulated during the present study. (see also Fig. 10).

COLORADO: Salida, Chaffee Co. (W. M. Wheeler leg.; MCZ); Canon City, Fremont Co. (Schmitt leg.; MCZ); Mesa Verde Nat. Pk. (A. C. Cole leg. and Coll., MCZ; B. Malkin leg. and Coll., MCZ); Trinidad, 6500 feet, 2 series (Cole leg. and Coll., MCZ). NEW MEXICO: Ute Park, Colfax Co., 7400 feet (2 series, Cole leg. and Coll., MCZ); Cimarron Canyon, 6 miles north of Ute Park, 7750 feet (Cole leg. and Coll., MCZ); 15 miles east of Taos, 8000 feet (Cole leg. and Coll., MCZ); 4 miles south of Los Alamos, 6400 feet (Cole leg. and Coll., MCZ); 5 miles south of Beulah, San Miguel Co., 7200 feet (Cole leg. and Coll., MCZ); Sapello Canyon, Beulah area, 8000 feet (Cole leg. and Coll., MCZ); Dailey Canyon, Beulah area (Cole leg. and Coll., MCZ); Bandelier Nat. Mon., 4 series at 6350 feet, 1 at 6050 feet

(Cole leg. and Coll., MCZ); Otowi Entrance, Bandelier Nat. Mon., 6100 feet (5 series, Cole leg and Coll., MCZ); Pecos (T. D. A. Cockerell leg.; MCZ); Albuquerque (MCZ); Mogollon Mt., Catron Co., 8600 feet (Cole leg. and Coll., MCZ). ARIZONA: Indian Garden and Coconino Forest, Grand Canyon (W. M. Wheeler leg.; MCZ); 20 miles north of Flagstaff (holotype nest series; also 1 series Cole leg. and Coll., MCZ); Flagstaff, south slope of San Francisco Peaks, 7000 feet (Wilson leg.; MCZ); Prescott (Wheeler leg.; MCZ); Oracle, Pinal Co., 4500 and 5000 feet (2 series, Wheeler leg.; MCZ); Stratton, Santa Catalina Mts., 6000-7000 feet (Wheeler leg.; MCZ); Miller Canyon, Huachuca Mts., 4800 and 5600 feet (2 series, Wheeler leg.; MCZ); Ramsey Canyon, Huachuca Mts. (W. S. Creighton leg. and Coll.); Campground, Chiricahua Mts., 5400 feet (Creighton leg. and Coll.); Campbell Blue Creek, Apache Nat. Forest (Creighton leg. and Coll.). DURANGO: 32 miles west of El Salto, 8700 feet (2 series, Creighton leg. and Coll.).

ECOLOGY. This species is limited to the lower altitudinal forest belts in the mountains of the Southwest, from juniper scrub at 7000 feet or less to mixed pine-spruce at 8000 feet. Judging from ecological notes accumulated by W. M. Wheeler, Cole, and myself, it nests almost exclusively under stones in dry, open situations. The type locality is situated in an area of open juniper scrub and scattered bunch-grass. *Sitiens* is co-dominant at this spot with several species of *Myrmecocystus, Pogonomyrmex*, and *Conomyrma*. At the base of the San Francisco Peaks, near Flagstaff, I found *sitiens* again abundant, nesting under rocks in open pine forest. In New Mexico Cole has taken *sitiens* primarily in pine forest and clearings bounded by pine forest. The ecological extremes in which he collected this species are as follows: near Los Alamos, a nest in an open, grassy area with scattered pine and juniper at 6400 feet; near Taos, a nest in moist pine-spruce woods at 8000 feet.

The light coloration, small eyes, and shortened appendages of *sitiens* constitute a remarkable morphological convergence to the species of the subgenus *Cautolasius,* and specifically to the primitive species *L.* (*C.*) *alienoflavus*. There can be little question that the characters shared by these two species are the mark of a subterranean mode of life. At the type locality I was unable to find any workers foraging above ground either during the day or in

the early night; in contrast, wherever the related species *neoniger* occurs its workers can nearly always be found above ground at any time of the day or night.

No nuptial flights of *sitiens* have been recorded. Reproductives have been taken *in nido* on six occasions, from July 2 (Campbell Blue Creek, Apache Nat. For., Ariz.) to July 30 (Bandelier Nat. Mon., N. Mex.). This would seem to indicate an early reproductive period similar to that of *L. crypticus.*

LASIUS ALIENOFLAVUS Bingham (Subg. *Cautolasius*)

Lasius alieno-flavus Bingham, 1903, The Fauna of British India (Taylor and Francis, London), Hymenoptera, **2**: 341; worker; queen; original description. Type locality: Indian Himalayas, above 8000 feet.

DIAGNOSIS. *Worker.* The three specimens examined are indistinguishable from northern Eurasian *flavus* of comparable size except for their longer maxillary palps and the fact that segment VI is longer than segment V. The right maxillary palp of a specimen in the MCZ measured as follows: segment III 0.15 mm., IV 0.11 mm., V 0.08 mm., VI 0.09 mm. *Flavus* workers of the same approximate size have much shorter segments: segment III probably never exceeds 0.13 mm., IV, 0.08 mm., V, 0.06 mm., or VI, 0.06 mm., and these segments are usually distinctly shorter. In this character *alienoflavus* actually overlaps the lower limits of the subgenus *Lasius: L. sitiens* workers of comparable size have approximately the same segment proportions.

TYPES. I have seen two workers in the AMNH and one in the MCZ labelled "N. Indien, I. XXXVII (Wroughton) / L. alieno-brunneus var. alieno-flavus For." From Bingham's description and comments it seems certain that these are part of the type nest series, but they were probably sent by Forel directly to Wheeler in the AMNH without first having been examined by Bingham. I do not think therefore it would be a valid procedure to select one as lectotype. The MCZ nidotype gives the following measurements: PW 0.51 mm., HW 0.76 mm., SL 0.70 mm., SI 92, EL 0.13 mm., ommatidium number 36 and 39. A second intercalary tooth is lacking in the one exposed (left) mandible. Petiole feebly emarginate. Cephalic pubescence dilute, as described for the eastern North American population of *flavus* (see

under geographic variation of that species). Head shape difficult to judge at this size, apparently "intermediate" (eastern North American *flavus-nearcticus*) approaching the *nearcticus* form, probably also within the range of variation of the Eurasian *flavus*. Otherwise identical to *flavus*. PW of AMNH nidotypes 0.44 and 0.48 mm.

Lasius flavus (Fabricius)

(Subg. *Cautolasius*)

Formica flava Fabricius, 1781, Species Insectorum, **1:** 491; worker; original description. Type locality: northern Europe.

Lasius brevicornis Emery, 1893, Zool. Jahrb. Syst., **7:** 639–640; worker, queen, male; original description. Type locality: District of Columbia; selected by Creighton (1950). NEW SYNONYMY.

Lasius flavus myops Forel, 1894, Bull. Soc. Vaud. Sci. Nat., **30:** 12; worker; original description. Type locality: Terni, Oran, Algeria. NEW SYNONYMY.

Lasius flavus var. *myops*, Emery, 1916, Bull. Soc. Ent. Ital., **47:** 167.

Lasius flavus myops var. *flavoides* Forel, 1894, *ibid.*, p. 12; worker; original description. Type locality: Fully, Switzerland. NEW SYNONYMY.

Lasius flavus var. *fuscoides* Ruzsky, 1902, Formicariae Imperii Rossici, Schrift. Naturforsch. Ges. Univ. Kasan, **38:** 281. Type locality: U.S.S.R. NEW SYNONYMY.

Lasius flavus var. *odoratus* Ruzsky, 1902, *ibid.*, pp. 282-283; worker; original description. Type locality: U.S.S.R. NEW SYNONYMY.

Lasius flavus var. *flavo-myops* Forel, 1915, Fauna Insect. Helv. Hym. Formicid. (Mitt. Schweiz. Ent. Ges., vol. 12), p. 52. NEW SYNONYMY (objective synonym of *flavoides* Forel).

Lasius brevicornis microps Wheeler, 1917, Proc. Amer. Acad. Arts Sci., Boston, **52:** 526; worker; original description. Type locality: Camp Curry, Yosemite Village, California, 4000 ft. NEW SYNONYMY.

Lasius flavus microps, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 422.

Formicina flava var. *morbosa* Bondroit, 1918, Ann. Soc. Ent. Fr., **87:** 28–29; worker, queen; original description. Type locality: France. NEW SYNONYMY.

Lasius umbratus var. *apennina* Menozzi, 1924, Atti Soc. Nat. Mat. Modena, **8:** 15; worker; original description. Type locality: Val Gorgo, Modena Apennines, Italy. NEW SYNONYMY.

Lasius flavus var. *apennina*, Menozzi, 1932, Boll. Ist. Ent. Bologna, **5:** 8–9.

Lasius umbratus ibericus Santschi, 1925, Eos, **1:** 349–350; worker; original

description. Type locality: Camprodón, Gerona, Spain. NEW SYNONYMY.

Lasius umbratus ibericus var. *sancho* Santschi, 1925, *ibid.*, p. 350; worker; original description. Type locality: Panticosa, Huesca, Spain. NEW SYNONYMY.

Lasius flavus var. *olivacea* Karawajew, 1926, Konowia, **5**: 194; worker; original description. Type locality: Turugai River, Dschewanschir region, Elizabethpol District, U.S.S.R. NEW SYNONYMY.

Lasius helvus Cook, 1953, The Ants of California (Pacific Books, Palo Alto, Calif.), p. 326, fig.; worker; original description. Type locality: Lake Tahoe, Calif. NEW SYNONYMY.

Lasius helveolus Cook, 1953, *ibid.*, p. 327. NEW SYNONYMY (objective synonym of *helvus* Cook).

DIAGNOSIS. *Worker and queen.* In the eastern United States, where *flavus* occurs sympatrically with *L. nearcticus*, it can be separated from this and other *Cautolasius* by a host of characters, but elsewhere these are subject to much geographic variation and tend to break down and lose their diagnostic value. Only one character has been found which will consistently separate all Nearctic and Palaearctic *flavus* populations from *nearcticus* (no. 1 below).

(1) Maxillary palp segment V as long as segment VI or longer.

(2) A much weaker character is found in the petiolar outline. In *flavus* the dorsal margin in frontal view is usually emarginate to flat, while in the majority of *nearcticus* it is convex.

(3) In addition, *flavus* can be separated from the related species *L. fallax* (Wilson) and *L. talpa* (Wilson) by the following character: scapes and outer tibial surfaces lacking standing hairs.

Male. Isolated individuals cannot be separated with certainty from other members of the subgenus.

(1) The subgenital plate tends to be subquadrate, with a protruding posteromedian setiferous area. This character will separate a majority of series from *nearcticus*.

(2) The outer femoral surfaces in *flavus* are ordinarily bare of standing hairs, separating this species from *fallax* and doubtfully from *talpa*.

FURTHER DESCRIPTION. *Worker.* (See also under geographic variation.) Mandibular dentition follows certain recognizable trends specific at least for the subgenus. In large specimens from northern Europe there are commonly four basal

teeth, with either the second or third from the base frequently reduced in size. As body size decreases the common basal tooth number becomes three and then two; in the latter case the median tooth is frequently reduced. Superimposed on this allometric variation is the frequent, non-allometric loss of the second intercalary tooth. Clypeus with a well defined median carina, which tends to become obsolescent in small workers. Anterior border of median clypeal lobe broadly and evenly rounded. Head tending to be more massive relative to body than in all other members of the genus with the exception of *L. brunneus*. Color highly variable, from straw yellow to dark yellowish brown. Minor workers are nearly aways clear yellow, medias show various degrees of light infuscation, and very large workers (found in northern Eurasia only) are often deeply infuscated.

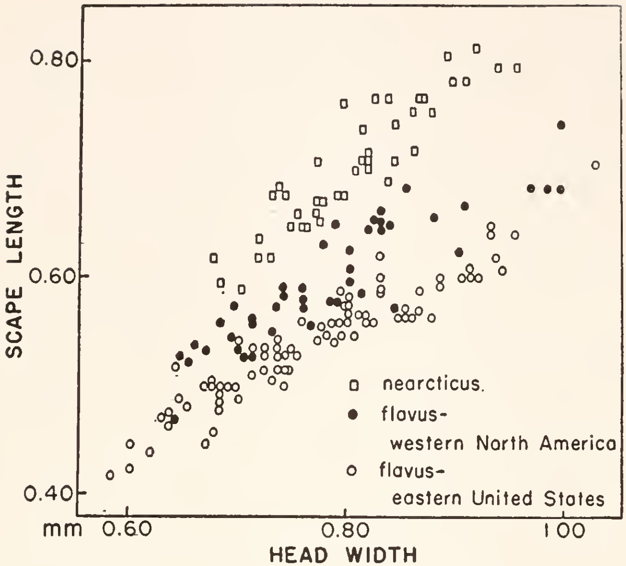
Male. Mandible form highly variable, ranging from the presumably primitive *sitkaensis* type to the *niger* type. The variation is partly allometric, i.e. the largest males usually have the *sitkaensis* type, while the smallest males always have the *niger* type or some degenerate modification of it.

GEOGRAPHIC VARIATION. *Forested eastern United States*. Throughout most of the forested portion of the eastern United States, *flavus* occurs sympatrically with the closely related species *nearcticus*. Within this range it consistently exhibits a set of characters which sharply distinguish it from *nearcticus* and set it off, at least statistically, from other *flavus* populations in North America and Eurasia. These characters, described in relation to *nearcticus*, can be summarized as follows:

(1) *Flavus* has a much shorter scape length; the SI-HW regression zones of the two species are well separated (Fig. 11).

(2) *Flavus* has a larger ommatidium number relative to HW; the regression zones of the two species are separate despite the fact that this is a very variable character (Fig. 11).

(3) *Flavus* has a head shape reminiscent of *L. brunneus:* in full face it is broader and tends to narrow more anterior to the eyes, while the mandibles are shorter, more incurved, and inserted closer to the midline. Of 39 series examined for this character, 34 showed the head shape just described and 5 were judged as intermediate to *nearcticus*. *Nearcticus* is more reminiscent of *L. niger:* the head is subquadrate, with well spaced, "typical" mandibles.



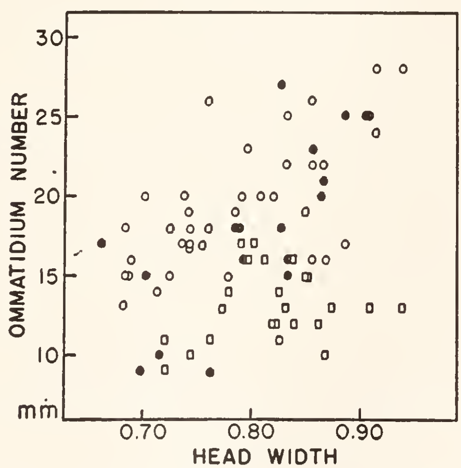


Fig. 11. Differential worker allometry in *L. nearcticus* and two geographic samples of *L. flavus*. Further explanation in the text. Nest series chosen at random; no more than three workers per series were measured.

(4) *Flavus* is more polymorphic, i.e. shows greater intranidal size variation. More than 90 per cent of *flavus* colonies were judged by the naked eye as feebly polymorphic, while the great majority of *nearcticus* colonies were judged as monomorphic.

(5) The palpal character previously described as diagnostic for *flavus* tends to be exaggerated in this population by a further shortening of segment VI relative to V. Thirty out of 34 nest series examined for this character contained at least some individuals with VI distinctly shorter than V.

(6) There is a tendency in *flavus* for a thinning of the cephalic pubescence. In more than 80 per cent of *nearcticus* nest series the margins of the head viewed in full face are covered with short, predominantly subdecumbent to erect pubescence dense enough to give a furry appearance. In *flavus* only 2 out of 11 series examined for the character showed this condition; 5 had the same type of pubescence but much sparser, so that stretches of the margin were nearly bare of it; 4 series were judged intermediate in the character.

(7) The queens of *flavus* are consistently larger. Since the head broadens allometrically with respect to the remainder of the body, this difference is best expressed in terms of the HW-thorax width relationship (Fig. 12).

Western North America. In the area encompassing southwestern Canada, Idaho, Washington, California, Arizona, and Colorado, where *nearcticus* is rare or completely absent, all of the characters above break down to some degree and the population of *flavus* converges toward *nearcticus*. Intermediate as well as extreme conditions occur in various combinations.

(1) The SI regression zone shifts upward to lie in an intermediate position between those of the eastern *flavus* and *nearcticus* (Fig. 11).

(2) The variability of the ommatidium number greatly increases, so that the broadened regression zone overlaps the eastern *flavus* and *nearcticus* zones (Fig. 11.).

(3) The *nearcticus* head shape comes to preponderate over that characterizing the eastern *flavus*. Of 21 series examined, 11 had the *nearcticus* head shape, 4 the head shape of the eastern *flavus*, and 6 were judged intermediate.

(4) Worker polymorphism becomes less common. Less than 50

per cent of the nest series were judged polymorphic with the naked eye.

(5) Maxillary palp segment VI elongates relative to segment V. Eighteen series examined had VI as long as V, whereas only 9 had VI shorter than V.

(6) The average density of cephalic pubescence increases. Of 22 nest series examined, 8 were similar to the typical *nearcticus*

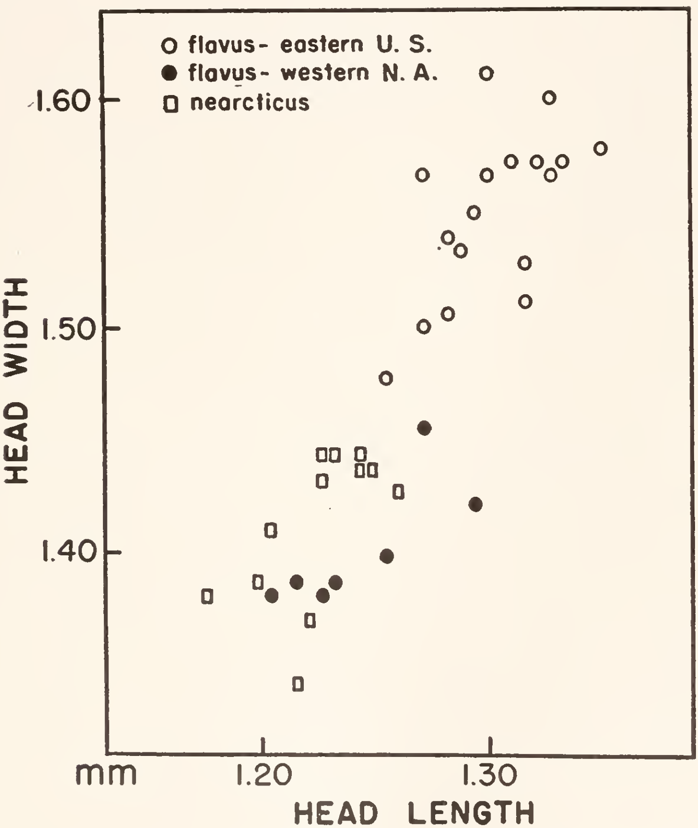


Fig. 12. Queen size variation and head length-head width allometry in *L. nearcticus* and two geographic samples of *L. flavus*. Further explanation in the text. Nest series chosen at random; no more than two queens per series were measured.

condition already described, 7 were similar to the eastern *flavus* condition, and 7 were judged intermediate.

(7) The queen size range decreases to about that of *nearcticus* (Fig. 12).

The picture of geographic variation in North America is an extraordinarily deceptive one. Lining up individual series in terms of character combinations, as I did at first, one easily gains a picture of two sympatric species in eastern North America and a single highly variable population, apparently of hybrid origin, in western North America. This impression is strengthened by the fact that the characters involved assort themselves independently in the western population. In fact, they occur in almost completely random combinations to produce what Anderson (1951) would call "discordant" variation and in higher plants at least associate with interspecific hybridization. The conclusion might be reached in this case that two sympatric species maintain themselves apart over a broad area in the east but have intergraded completely in an adjacent, equally broad area in the west. Such an anomalous situation is not without precedent in taxonomic literature. It has been described in Asiatic butterflies of the genus *Karanasa* (Avinoff and Sweadner, 1951), and for Chinese composites of the genus *Ixeris* (Stebbins, 1950).

Detailed analysis has revealed that this explanation is not the correct one for *Lasius flavus*, however. The clue which led to the alternative explanation, that the western population is a highly variable, but nevertheless pure *flavus* population, came from the SI and palp characters. Unlike the other characters, the SI remains relatively constant in the west, despite the fact that its regression zone is intermediate between the eastern *flavus* and *nearcticus*. One does not find the great spread in variability ordinarily encountered in introgressive hybridization. The palp character presents even more suggestive evidence. Although it converges away from the eastern *flavus* toward *nearcticus*, it converges only up to a point, and it is the only character of the assemblage which preserves a discontinuity. On the basis of the palp character by itself it appears that the western intermediate population is composed almost entirely of *flavus*.

This conclusion is supported by the fact that the southern European population of *flavus* is very close to that in western North America and varies almost as randomly. Were the western North

American population to be considered as having originated through interspecific hybridization, then the southern European population would have to be explained as a migratory extension of the North American population. This is, on any grounds, a most unlikely hypothesis, particularly in view of the fact that most of the "hybrid" variability is still preserved half way around the world from the point of contact between the two "parents".

The western population was finally proven to be *flavus* by an

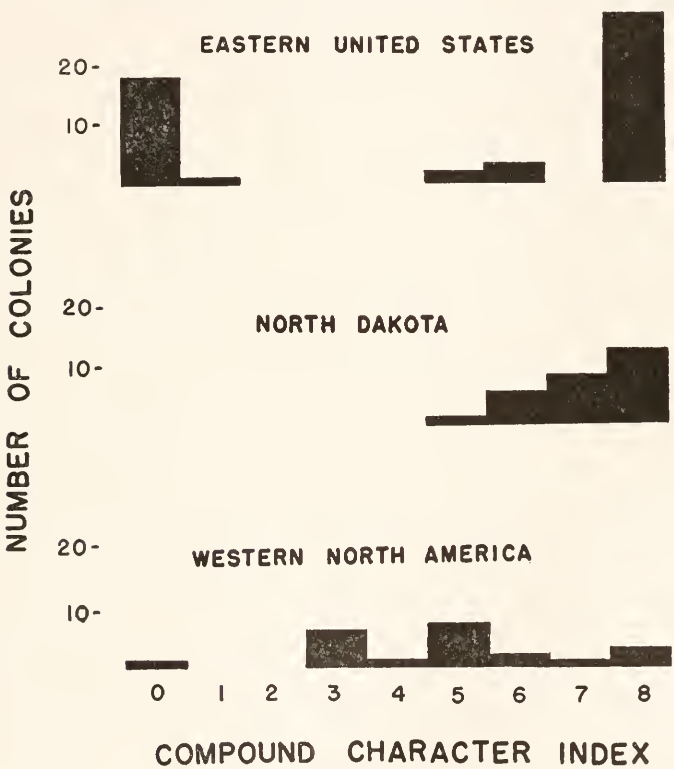


Fig. 13. Frequency histograms of the compound character index of *L. nearcticus* (0-1) and *L. flavus* (3-8) in three geographic samples, illustrating the presumed effect of interspecific competition on geographic variation in the latter species. Further explanation in the text.

analysis of material from many localities in North Dakota, which state includes in its eastern half the transition belt between grassland and deciduous forest; this belt presumably carries the western outliers of the *nearcticus* population. If all of the material from the state is treated as a unit, *flavus* is caught in the very process of shifting from the divergent eastern condition to the more *nearcticus*-like western condition. This population is intermediate between the eastern and western populations when all of the characters are taken together, and it does not exhibit any feature of variation which would indicate hybridization with *nearcticus.*

I have illustrated this remarkable geographic variation in Figure 13 by means of a ''compound character index'', which is identical to the ''hybrid index'' of Anderson (1949), except that species convergence, and not hybridization, is involved. In this graph, typical *nearcticus* characters are each given a score of 0, typical eastern *flavus* characters 2, and intermediate characters 1. The four characters most consistent in the eastern population are used: maxillary palp, scape index, ommatidium number, and head shape. Completely typical *nearcticus* nest series score a total of 0 and completely typical eastern *flavus* 8, with the various ranks of intermediates falling in between.

It is my opinion that competition with *nearcticus* is the major influence effecting this variation in North America. Across Eurasia and western North America *flavus* is mostly intermediate in morphology between the two extreme forms, and in several of the important characters it overlaps *nearcticus* broadly; it is consistently different from *nearcticus* only in the palp character. In the forests of eastern North America it meets *nearcticus* and immediately diverges from it in six additional characters.

It is a well known principle of ecology that two closely related species can succeed in the same geographic area only if they show some ecological difference which prevents their coming into direct and absolute competition. Expressed in another and perhaps more appropriate way, it is to be expected that any ecological difference of two sympatric series will be to their advantage and will be selected if it has a genetic origin (Mayr, 1949a). Increased ecological divergence resulting from selection can be expected in turn to have some collateral effect on the morphology of the species involved. This is the process which I believe has

been operative in the profound morphological changes in the eastern North American *flavus*.

There can be little doubt that *flavus* and *nearcticus* are ecologically different where they occur together. Of nine eastern *flavus* collections for which I have data, seven were taken in what may be collectively called open dry woods and two in open moist woods. Of eleven *nearcticus* collections, three were taken in open moist woods and eight in dense moist woods. *Flavus* seems to be able to thrive in bare or poorly covered earth, while *nearcticus* is mostly limited to earth with thick litter and humus cover. There is little information available to tell us whether the western population of *flavus* shows the expected overlapping ecological range. I found this ant abundant on the eastern slopes of the Sierra Nevada, in the vicinity of Yosemite Valley, nesting mostly in open conifer forest with relatively dry soil but under a wide variety of shade conditions. There were few moist woodland situations available at the elevations at which *flavus* occurs. In Europe *flavus* favors open situations but also occurs in moist woodland (see under Ecology).

Maritime Canada. Flavus from this area, roughly north of the 45th parallel, do not seem to conform well with the remainder of the eastern population. Series from Pleasantfield and North Brooksfield, Nova Scotia, and Penobsquis, New Brunswick, have intermediate scape indices. Another series from Pleasantfield has small, "*nearcticus*" eyes. Significantly, *nearcticus* is not known to occur this far north.

Aberrant North American series. Seven nest series encountered among the North American material have presented difficulties in species placement by the palp character. A series of *nearcticus* from Boston, Mass. (W. M. Wheeler leg.; MCZ) has one individual in five with segment V as long as segment VI, the *flavus* condition; another series, from Blind River, Ont. (Wilson leg.; MCZ), has one individual in four with the same condition. Series determined as *flavus* from Garrison, McClean Co., N. Dak. (R. P. Uhlmann leg.; G. C. Wheeler Coll.) and Divide Co., N. Dak. (2 series, J. David leg.; G. C. Wheeler Coll.) have single individuals with segment VI longer than segment V on one palp. In these several cases there is no evidence that hybridization has played a part; all involve single aberrant individuals from otherwise normal nest series. The following two cases are somewhat more

difficult to explain. A series from Tar Island, Rockport, Ont. (W. S. Creighton leg. and Coll.) has *nearcticus* palps, intermediate head shape and scape index, and *flavus* eyes. A second series from nearby Buck Island (Creighton) has *nearcticus* palps, intermediate head shape and scape index, and *nearcticus* eyes. Both of these series have been determined tentatively as aberrant *nearcticus;* perhaps they represent a divergent trend in this species at the northern periphery of its range.

Concordance of character variation in North America. As described above, the combination of characters marking the eastern population of *flavus* seems to be closely associated with the distribution of *nearcticus;* they are rapidly modified when *nearcticus* is left behind at the edge of the deciduous forest. The four characters used in the compound character index of Figure 13 exist in the eastern *flavus* condition in a series from Devils Tower, Wyoming (Creighton leg. and Coll.), which is the westernmost known locality for *nearcticus.* They also exist in a series from Gregory Canyon, Boulder, Colo. (Creighton leg. and Coll.) and San Geronimo, N. Mex. (M. Cooper leg.; MCZ), which two localities are conceivably within the range and ecological influence of the *nearcticus*-like species *fallax,* although there is an admitted danger of overstretching a point by bringing this species into the discussion.

The shift of characters in *flavus* from east to west is partly observable in the North Dakota series (mostly G. C. Wheeler Coll.). In this area these characters are really discordant, in that some have been observed to shift to the western trend while others have not. Specifically, if the North Dakota series are treated as a unit (they are too incomplete to show trends within the state), they resemble the western population in queen size and worker palp character and the eastern population in worker eye size and head shape, but show a highly variable mixture of low and intermediate scape indices.

Northern Europe. In Britain, Scandinavia, France, Benelux, and Germany, judging from several dozen series examined, the workers average larger in size than elsewhere and are much more polymorphic, i.e. show greater intranidal size variation and attain larger maximum size. The size frequency curve of a single Scottish nest series (Fig. 14) shows a trend toward bimodality, a characteristic of primitive types of worker polymorphism in

general and the most extreme development of this phenomenon in the genus. In addition, these northern series have greater relative eye size and higher scape indices than any other populations. The SI regression zone, in fact, is nearly coincidental with that of *nearcticus.* Queen size is small, closer to the western North American population than to the eastern.

Central Europe and the Mediterranean perimeter. Abundant material, primarily from Italy, Yugoslavia, and North Africa, shows greatly decreased polymorphism, along with diminished relative eye size. Abundant material from Switzerland is clearly intermediate in all three characters, showing the extreme as well as the intermediate conditions in various combinations.

Eastern Asia. Specimens from this area closely resemble the northern European form. Workers from Mt. Akagi (Akagisan), Honshu (MCZ); Nikkō, Honshu (E. Silvestri leg., MCZ; H. Okamoto leg. and Coll.); and Hirooka, Shikoku (Okamoto leg. and Coll.) are long-scaped and large-eyed. Workers from Miao T'ai Tze, Shensi, China (W. L. Brown leg.; MCZ) are long-scaped and small-eyed. Queens from Tokyo (L. Gressitt leg.; MCZ) have HW's of 1.41, 1.44, and 1.47 mm., and a queen from

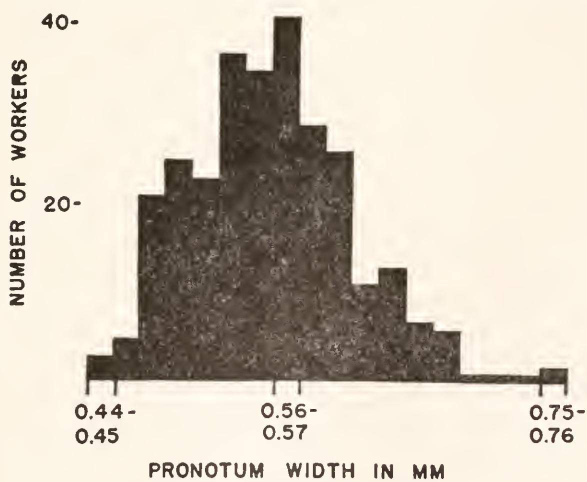


Fig. 14. Size frequency distribution of the workers of a single nest series of *L. flavus* from Kilchattan Bay, Bute, Scotland. Note the skewness characteristic of the early phylogenetic stages of worker polymorphism.

"Eastern Tomb" (Nanking?) (Chi Ho leg.; MCZ) has a HW of 1.42 mm., all consistent with the European population.

Racial divisions. For the benefit of those who insist on applying trinomens to different segments of the population, I believe it is safe to say that the only workable division which can be made is between the eastern North American population ("*flavus brevicornis*") and the rest of the species ("*flavus flavus*"). The western North American population is exceedingly close to that of Italy and North Africa, differing only in having larger eyes, longer scapes, a slightly greater tendency toward polymorphism, and a frequent occurrence of the "*nearcticus*" head shape (absent in Europe); there is wide overlap in these characters admitting of no subspecific division by conventional standards (cf. Mayr, Linsley, and Usinger, 1953). The southern and northern European segments differ by several characters, including degree of polymorphism, scape length, and eye size, but there is a wide zone of transition between them, and, more important, the western North American population falls intermediate between the two in every character.

DISTRIBUTION. *L. flavus* has a very wide range through Eurasia and North America, exceeded within the genus only by that of *L. alienus*. According to Donisthorpe (1927) *flavus* occurs throughout England and reaches into southern Scotland; I can supply the following supplementary records from southern Scotland: Aberfoyle (MCZ); Kilchattan Bay, Bute (M. V. Brian leg.; MCZ); Glen Luss, Dumbarton (Brian leg.; MCZ); Ballochraggen, Stirling (Brian leg.; MCZ); North Berwick (Brian leg.; MCZ). In Ireland, according to O'Rourke (1950) *flavus* reaches northward to Malin Head on the coast and to south of Dublin inland. Holgersen (1944) has taken it in Norway north to Vågå, Opland. Forsslund (1947) has found it in southern, central, and eastern Sweden north to Västerbotten Province and southeastern Lappland; I have determined material in his collection originating from as far north as Luleå, Norrbotten. The species reaches southern Finland (Helsinki; Forsius leg.; MCZ) and probably extends eastward across the northern part of European Russia. The large amount of material I have examined from western Europe, coupled with numerous local faunal reports in the literature, indicate that *flavus* is abundant from southern Scandinavia as far south as the mountains of central

Italy. It occurs in northern Spain (Menozzi, 1922), and I have seen material from southern Italy (Sambiase, Calabria; MCZ), numerous localities in northern and central Yugoslavia (all MCZ), Albania (Tomorica; Ravasini and Lona leg.; MCZ), and Lebanon (mountain above Kammouha Plain, 1500 meters, winged queens and males; K. Christiansen leg.; MCZ). I have determined series from the following North African localities: Azrou, Morocco (W. M. Wheeler leg.; MCZ); Tachdirt, Morocco (R. Koch leg.; MCZ); Terni, Oran, Algeria (*myops* Forel syntypes). So far as I know *flavus* has never been taken in the Balearics, Canaries, Azores, or on Madeira. It occurs in the Caucasus (Schneider leg.; MCZ). According to Karawajew (1931) it occurs fairly far north in Siberia, reaching the Tomsk and Yenisei Districts, the Akmolinsk region, the Yakutsk District (north to Ust Kut), and Kamchatka. One gains the impression from the literature that *flavus* is rare or absent around most of the Tibetan Plateau. Kusnetzov-Ugamskij (1929a) states that it occurs in the Tien Shan, but is scarce there and limited to high elevations. Menozzi (1939) did not find it in the substantial collections of the genus made in the Karakoram and western Himalayas by the Duca di Spoleto expedition. Eidmann (1941) found a single series of "*myops*" in the collections of the Brooke Dolan expedition to the eastern rim of the Tibetan Plateau, but this may well be *talpa* Wilson instead of *flavus*. The several eastern Asiatic records verified during the present study have already been presented in the section on geographic variation.

In North America *flavus* is distributed similarly to *L. umbratus,* being abundant through most of the eastern half, declining in the southern Rockies, and becoming rare or absent in the northern Rockies and Pacific Northwest. It differs from *umbratus* in being abundant in the Sierra Nevada of California. I have compiled the following records from southeastern Canada: Blind River, Ont. (E. O. Wilson leg.; MCZ); Ottawa, Ont. (USNM); Hull, Quebec (W. M. Wheeler leg.; MCZ); Penobsquis, New Brunswick (C. A. Frost leg.; MCZ); Pleasantfield and North Brookfield, Nova Scotia (W. H. Prest leg.; MCZ). Numerous field observations by the present writer, local faunal studies published by others, and the abundance of material in collections suggest that *flavus* is a common species throughout the eastern United States south to the mountains of North Carolina and

Tennessee. It is rare in the Gulf States; I have collected it at Peterson and Brookwood, Tuscaloosa Co., Ala. (MCZ), while Smith (1931) has recorded it from Ripley, Tippah Co., Miss. Westward, Buren (1944) found it common in Iowa, while the collections of G. C. Wheeler and his students contain numerous series from over all of North Dakota.

I append the following western records, exclusive of North Dakota, compiled during the present revision. SOUTH DAKOTA: Pierre (W. M. Wheeler leg.; MCZ); Hot Springs, Fall River Co. (MCZ); Hill City (T. Ulke leg.; USNM). WYOMING: Devils Tower, Crook Co. (W. S. Creighton leg. and Coll.). SASKATCHEWAN: Farewell Creek (MCZ). ALBERTA: Banff (subsp. *claripennis* Wheeler syntypes). IDAHO: Bloomington Ridge, Wasatch Range, 9000 feet (B. Malkin leg. and Coll., MCZ). COLORADO: Gregory Canyon, Boulder (Creighton leg. and Coll.); Topaz Butte, Florissant, Teller Co., 9000 feet (W. M. Wheeler leg.; MCZ); Cheyenne Canyon, Colorado Springs (MCZ); Canon City, Fremont Co. (Schmitt leg.; MCZ); Creede, Mineral Co., alate queen (MCZ). NEW MEXICO: between Raton Pass and Raton, Colfax Co., 7100 feet (A. C. Cole leg. and Coll., MCZ). ARIZONA: Soldier's Camp, Santa Catalina Mts., 7700 feet (L. F. Byars leg. and Coll., MCZ); Mt. Lemmon, Santa Catalina Mts., 9150 feet (W. M. Wheeler leg.; MCZ). NEVADA: Lehman Caves, Mt. Wheeler (Creighton leg. and Coll.). CALIFORNIA: Sequoia National Park (Creighton leg. and Coll.); Kings Canyon National Park (J. H. Eads leg.; MCZ); Dalton Creek, Fresno Co., 4800 feet (H. Dietrich leg.; specimen lost); Camp Curry, Yosemite National Park, 4000 feet (subsp. *microps* Wheeler syntypes; also Wilson leg.; MCZ); Mariposa Grove, Yosemite National Park, 6500 feet (Wilson leg.; MCZ); 14 miles west of Dardanelle, Tuolumne Co., 6500 feet (Wilson leg.; MCZ); Twain-Harte, Tuolumne Co. (F. E. Blaisdell leg.; CAS); Lake Tahoe (*helvus* Cook types; also W. M. Wheeler leg., MCZ). OREGON: Mt. Hood, 6500 feet (Cole Coll.). WASHINGTON: Cle Elum, Kittitas Co. (T. Kincaid leg.; Cole Coll.); Pullman (W. M. Mann leg.; MCZ).

ECOLOGY. The nesting habits and habitat preferences of *flavus* are subject to marked geographic variation. In Germany, Gösswald (1932) found the species to be highly adaptable, occupying moist forest floors, forest borders, hedgerows, grassy paths,

and sparsely vegetated wasteland. It is able to penetrate into cultivated areas but does not nest in gardens. In a random field sample, Gösswald recorded 835 colonies under stones, usually in dry situations, 300 in mounds, mostly in meadows, and 30 in dead tree trunks in woodland. The mounds reach their largest size in swampy areas, and may exceed 60 cm. in height. Gösswald judged this species to be more adaptable, although not more abundant, than *L. niger*. He encountered 6 colonies that he determined as "*myops*", all under rocks in open, dry ground. It sounds likely that these were depauperate colonies living in a habitat affording only marginal existence.

Many other authors have made similar observations concerning the diverse nesting habits of *flavus* in northern and central Europe. O'Rourke (1950) found it in Ireland mostly in dry, sunny situations with fine soil, but never encountered it in marshes or in rotting wood in forests. Skwarra (1929) found it to be a very successful ant in the Zehlau Moor of East Prussia, exceeded in abundance there only by *L. niger;* she notes the general preferences of this species for open, moist, grassy land, in fields, marshes, along the shores of inland lakes and ponds, and on riverbanks.

The mounds which the European *flavus* builds have been described in the literature many times. In Switzerland they occur mostly on eastern and southern mountain slopes, tending to increase in height and size with elevation (Wheeler, Forel, *et al.*). They are typically elongate in shape under these conditions, with the long axis east-west and the east face precipitous. According to Linder (1908) this peculiar shape is caused by the ants inhabiting and building only in the east end of the mound.

In southern Europe, in the lowlands at least, the mound-building habit is lost, and the species nests almost exclusively under stones. Zimmermann (1934), for instance, found it limited to this latter nesting site in the islands around the Quarnerolo. At Miao T'ai Tze, Shensi, China, W. L. Brown (pers. commun.) found *flavus* nesting under stones. This is the only type of nesting site I encountered in several dense populations in the Sierra Nevada of California, and is by far the predominant type through the eastern U.S. I do not know of any cases in North America of *flavus* constructing mounds in open soil.

European observers are in agreement that *flavus* is completely subterranean. Its mounds ordinarily lack external openings and workers are rarely seen above the ground. In Ontario and California I watched for signs of activity around *flavus* nests at night, but was never rewarded with the sight of a foraging worker. It has been generally assumed that the main food source of this species consists of the secretions of Homoptera maintained in the nests (cf. Eidmann, 1926), but food habits have never been well investigated. Indeed, I have only occasionally found evidence of any food source, including Homoptera, in a number of nests I have excavated, although workers and brood were turned up in abundance. The utilization of some amount of insect food seems likely. Donisthorpe (1927, p. 258) mentions the presence of insect remains in *flavus* galleries under stones, and Richards (1953, p. 128) has observed *flavus* workers dismembering a caterpillar on top of a mound.

The mass of published data on nuptial flights by this species in Europe has been well summarized by Donisthorpe (1927). The flights occur in the late afternoon from July to September and predominantly in August. They are often concurrent with flights of *L. niger*. Winged forms are found in the nests from June to October. I have seen *in nido* North American collections of winged forms ranging from July 21 (Penobsquis, New Brunswick) to August 30 (Rochester, New Hampshire).

SYNONYMY. *Lasius brevicornis* Emery. Lectotype by present selection, a queen in the MCZ labelled "Georgetown, D. C., Coll. Hill, Aug. 10, 85, under stone." This specimen is typical for the eastern North American population of *flavus* in head width (1.61 mm.) and in the maxillary palp (segment V longer than VI). A worker syntype in the MCZ from Cuckoo, Va., is typical for the eastern population in all of the characters previously described. This is the available and appropriate name if a trinomen for the population is to be applied at all.

Lasius flavus myops Forel. Lectotype by present selection, a worker in the MCZ labelled "Terni, 9/IV." PW 0.50 mm., HW 0.73 mm., SL 0.59 mm., SI 81, ommatidium number 29 and 26, maxillary palp segment VI as long as V. SI and ommatidium number consistent with the southern European-North African population, but *myops* is not applicable as a trinomen since this population cannot be given subspecies rank even by

conventional standards. The simple allometric basis for reduction in eye size in this form was first recognized by Emery (1915), but to van Boven (1951) must go the credit for first demonstrating the relationship by precise measurements.

Lasius flavus myops var. *flavoides* Forel. This is the first name applied to the form intermediate between *flavus* and *myops*. It was characterized as having an ommatidium number of about 30. Syntypes in the AMNH are typical small *flavus* workers.

Lasius flavus var. *fuscoides* Ruzsky. This name was proposed to cover specimens from European Russia, the Caucasus, and Siberia with brown to reddish brown heads and gasters. Although I have little material from this area and no types, I am convinced that *fuscoides* is nothing more than the darker form of major worker which also occurs through the Balkans and western Europe.

Lasius flavus var. *odoratus* Ruzsky. This mysterious variety was based primarily on its odor, said to resemble an "aromatic geranium." In addition, the scale was described as narrower toward the top than in the typical *flavus*, but this is a very variable structure within the species and of dubious taxonomic value. Kuznetzov-Ugamskij (1929a) comments that all of the many series of *flavus* which he collected in the Ussuri region of southeastern Siberia possessed a distinct aromatic odor and could be included in Ruzsky's variety. In tentatively assigning this variety to the synonymy of *flavus*, I must point out that it may represent a distinct cryptic sister species instead.

Lasius brevicornis microps Wheeler. Lectotype by present selection, a worker in the MCZ. PW 0.52 mm., HW 0.77 mm., SL 0.62 mm., SI 81, ommatidium number in both eyes 15. The reasons why this form cannot be upheld even by conventional subspecies standards have already been made clear in the section on geographic variation.

Formicina flava var. *morbosa* Bondroit. The principal characters given for this variety were longer scapes and larger eyes in a small, uniform worker caste. Bondroit thus chose three of the most variable characters in the western European population. There is nothing in the description to indicate that *morbosa* falls outside the normal range of variation of *flavus*.

Lasius umbratus var. *apennina* Menozzi. When, after eight

years, Menozzi realized he had determined the *apennina* types to the wrong species, he was hard put to find a character with which to salvage his varietal name. The one he did use, erect hairs present on the tibiae, is an infrequent but normal variation encountered in the western European population.

Lasius umbratus ibericus Santschi. Lectotype by present selection, a worker in the Santschi Collection. PW 0.76 mm., HW 1.17 mm., SL 0.92 mm., SI 79. Two additional syntype workers in the same collection were examined. This series is typical *flavus*, possessing characteristic metapleural gland openings (excluding it from *Chthonolasius*), polymorphism, petiolar scale, coloration, pilosity, etc.

Lasius umbratus ibericus var. *sancho* Santschi. This form was described as nothing more than a trivial variant of *ibericus*.

Lasius flavus var. *olivacea* Karawajew. This variety is supposedly distinguished by the possession of a dirty olive-green overtone to the normal color and by slightly broader scapes. I have never seen material fitting this description and suggest synonymy in this case only tentatively.

Lasius helvus Cook. Holotype and one paratype in the Cook Collection, one paratype in the MCZ. Through the courtesy of Dr. Cook I have been allowed to examine all three of the type specimens. This species is a clearcut synonym of *L. flavus* and does not deviate in any way from the western North American population. To avoid possible confusion in the future I must point out that the figures accompanying the original description are badly in error with respect to scape length, eye size, and alitrunk shape. Also, the size (PW 0.47 mm.) is not unusually small, as was claimed by Dr. Cook.

Lasius fallax Wilson, new species

(Subg. *Cautolasius*)

DIAGNOSIS. A population inhabiting the Rocky Mountains and Great Basin from Idaho and Montana south to southern Arizona, almost exactly intermediate in each of the critical diagnostic characters separating *flavus*, *nearcticus* and *talpa*. Because it is parapatric with *nearcticus*, the possibility exists that it represents a western variant of that species, but for several

reasons to be given later, it has been treated herein as a distinct species.

Worker. (1) Outer surfaces of the tibiae with numerous standing hairs prominent above a dense ground pubescence. Scapes with dense standing pubescence grading into hairs of intermediate length ($\frac{1}{4}$-$\frac{1}{2}$ $\times$ as long as the maximum scape width) but with few or no outstanding hairs along the plane of count.

(2) Relative lengths of the two terminal segments of the maxillary palp very variable within individual nest series, grading from the *flavus* condition (segment V equal to or longer than segment VI) to the *nearcticus* condition (segment V shorter than segment VI). The *flavus* condition usually preponderates, and the *nearcticus* condition may be altogether absent in any single nest series.

(3) The allometric regression zones for both ommatidium number and scape length relative to head width appear to be exactly consistent with those for the western North American population of *flavus,* which is intermediate between *nearcticus* and the sympatric eastern population of *flavus.* The minimum recorded ommatidium number is 12, higher than in the majority of *talpa* series.

Queen. Appendage pilosity as in worker. Terminal maxillary palp segments as in *flavus,* varying within single nest series from segments V and VI equal in length, to V longer than VI. Size variation similar to that of *nearcticus* and western North American-Eurasian *flavus;* HW 1.38-1.55 mm. Color similar to *flavus,* darker than *talpa.*

Male. At least 2 or 3 and usually more than 6 standing hairs along the outer lateral femoral surfaces; in *nearcticus* rarely more than 1 or 2 and usually none. Mandible form varying as in other *Cautolasius.*

HOLOTYPE. A worker in the Creighton Collection selected from a series collected at Bassets Springs, Uinta Mts., Utah, with associated winged queens and males (W. S. Creighton leg.). PW 0.50 mm., HW 0.72 mm., SL 0.57 mm., SI 79, ommatidium number 19 and 27. Paranidotypes are in the MCZ.

FURTHER DESCRIPTION. *Worker.* PW range 0.44-0.70 mm., maximum intranidal range 0.44-0.56 mm. (Hartzel, Colo.) and 0.49-0.67 mm. (Kaibab Nat. For., Ariz.). Head shape usually more like that of *nearcticus* than *flavus,* i.e. subquadrate with

widely spaced mandibles; intermediate in the Monticello, Utah series. Cephalic pubescence as in *nearcticus*. Mandibular dentition similar to *nearcticus,* showing part of the *flavus* variation; two basal teeth always present, occasionally with a third, intercalary tooth, and a second intercalary tooth present in all specimens examined. Color of body and appendages medium yellow to very light yellowish brown, head often a shade darker than the rest of the body.

Male. Subgenital plate of male from Lost River Range, Idaho, subquadrate, with a single prominent median setiferous lobe. Lacking the extended posterolateral flanges of *talpa*.

GEOGRAPHIC VARIATION. The known range of *fallax* overlaps that of *flavus* in Washington, Idaho, central Colorado, and northern Arizona, and it is almost perfectly contiguous with that of *nearcticus*. The possibility therefore exists that *fallax* represents a population of *nearcticus* which has shifted in its morphology in a direction toward *flavus,* just as *flavus* shifts toward *nearcticus* in North Dakota and the Far West. This possibility is strengthened by the fact that the *fallax* pilosity character is weakest, and may even be considered intermediate to *nearcticus,* in the two series (Glacier Nat. Park and Hartsel) taken closest to the known *nearcticus* range.

Nevertheless, I have decided to regard this population as a distinct species for the following reasons. It has not been established in the first place that *fallax* is not really a population of *flavus,* since they have never been taken together in the same immediate locality, and they are perhaps even closer to one another morphologically than *fallax* and *nearcticus*. To include *fallax* in *nearcticus* on the basis of available material would be an arbitrary step which would greatly complicate the already confusing diagnosis of *nearcticus;* the reason for this is that the one pristine *nearcticus* character, that of the relative lengths of the terminal maxillary palp segments, breaks down in *fallax*. Also, while the Glacier National Park and Hartsel series approach *nearcticus* in pilosity, they do not approach it in the palpal, scape, and eye characters; all of the *fallax* series are consistent in these three characters. Future collecting may prove me wrong, but it appears at the present time that the most stable and practical classification will be one in which *fallax* is segregated as a full species.

DISTRIBUTION. Over 200 workers, 16 queens, and 13 males were examined from the localities listed below. Except for the Washington and Glacier National Park series, all collections were made by Dr. W. S. Creighton, and the bulk of the type material is in his collection.

WASHINGTON: Huntsville, Columbia Co. (A. C. Burrill leg.; MCZ); Kamiak Butte, Palouse, Whitman Co. (A. C. Burrill leg.; MCZ). IDAHO: Double Springs Summit, Lost River Range, winged queens and males VIII-22-1933. MONTANA: Lake McGregor, Flathead Co.; St. Marys Entrance, Glacier Nat. Pk. (E. O. Wilson leg.; MCZ). WYOMING: 20 miles east of Moran. COLORADO: Hartsel, Park. Co. UTAH: Bassets Springs, Uinta Mts. (holotype nest series); Deep Creek, Uinta Mts.; Warner Ranger Station, La Sal Mts., males VII-19-1933; Monticello, Blue Mts., winged queens and males VII-30-1933. ARIZONA: Kaibab National Forest, Grand Canyon.

ECOLOGY. The Glacier National Park series was taken from a populous colony nesting under a stone in a clearing in a pine-fir forest at about 5000 feet. *Lasius sitkaensis* was abundant in the same immediate area, under stones in clearings as well as in rotting logs in the forest. *L. crypticus* also occurred in the clearings under stones.

Lasius nearcticus Wheeler

(Subg. *Cautolasius*)

Lasius flavus nearcticus Wheeler, 1906, Psyche, **13**: 38–39; worker; original description. Type locality: Illinois, by selection of Creighton, 1950, Bull. Mus. Comp. Zool., **104**: 422.

DIAGNOSIS. *Worker.* (1) Segment VI of the maxillary palp distinctly longer than segment V.

(2) Scape long, always surpassing the occipital border by a considerable margin, the SI-HW regression zone well above those of the majority of series of other *Cautolasius* with the exception of the northern Eurasian population of *flavus* (Fig. 11).

(3) Eyes small relative to head size, ommatidium number usually 9 to 17, but still averaging larger than in *talpa* (Fig. 11).

(4) Differing from the sympatric eastern North American population of *flavus* by a number of other distinctive characters

which break down in the allopatric western North American and Eurasian populations of *flavus* (see the section on geographic variation in that species).

Queen. (1) Usually sharing the maxillary palp character of the worker. Single, exceptional, individuals from nest series from Catawba, Ohio (M. Amstutz leg.; Talbot Coll. and MCZ) and McGregor Lake, Quebec (F. J. O'Rourke leg.; MCZ) have segment V equalling segment VI in length on one side only.

(2) Differing in size from the sympatric eastern North American population of *flavus* (see under *flavus*).

Male. The diagnostic palpal character of the worker and queen is not shared by this caste; segment V is usually as long as VI and occasionally longer, the relative lengths showing considerable intranidal variability. The only possible distinctive character I have encountered is in the subgenital plate. In several *nearcticus* series examined it is shaped like a rectangle bent posteriorly, so that the anterior border is evenly convex and the posterior border evenly and deeply concave. The posteromedian setiferous area tends to be less prominent than in other *Cautolasius* and is one- or two-lobed. The subgenital plate of *flavus* is typically subquadrate in shape, although series from the Chilhowee Mountains of Tennessee are indistinguishable from *nearcticus,* while the plate figured by Clausen (1938) from Zurich is intermediate.

TYPES. The location of Wheeler's syntypes is unknown. The original description mentions workers from Illinois, Massachusetts, Connecticut, New York, and New Jersey, and it is possible that determined series in the MCZ from Colebrook, Conn. (Wheeler) and Woods Hole, Mass. (A. M. Field) were among the ones originally studied. For no stated reason Creighton (1950) selected Illinois as the type locality, even though no Illinois material is in the determined Wheeler collection. Since definitely authentic material may yet be discovered, it would be very unwise at this point to recognize any specimens as syntypes and to select a lectotype. Fortunately, Wheeler's description of the worker, his later determination of material in the MCZ, and his comments on the ecology ("only in damp soil in shady woods") leave little doubt that the present assignment of the name is correct.

FURTHER DESCRIPTION. PW range 0.45-0.64 mm., maxi-

mum intranidal size variation 0.45-0.58 mm. (Gibraltar Island, Ohio; M. Amstutz leg.; Talbot Coll.). Apparently the least size-variable and most monomorphic of the four better known *Cautolasius* species. Mandibular dentition showing part of the variation seen in *flavus:* two well-developed teeth present and often a third, intercalary tooth in addition; the regular second intercalary tooth present in all specimens examined. Head covered with a dense ground pubescence, which obscures the margins of the head viewed in full face; this character also occurs in *talpa* and *fallax* but is only occasional in *flavus*. Color pale to medium yellow, the gaster often lighter than the alitrunk and the alitrunk lighter than the head; averaging and ranging over-all lighter than other members of the subgenus.

Male. Mandible form showing the same extreme range of variation as in *flavus*, from the "*sitkaensis* type" to the "*niger* type."

DISTRIBUTION. This species is common throughout most of the forested area from southeastern Canada to the southern Appalachian mountains. It is occasional as far west as South Dakota and Wyoming. Specific Canadian records accumulated during the present study are as follows: Kingsmere, Que. (W. M. Wheeler leg.; MCZ); Lake McGregor, Que. (F. J. O'Rourke leg.; MCZ); Hull, Que. (Wheeler leg.; MCZ); Arnprior, Ont. (C. Macnamara leg.; USNM); Tar Is. and Buck Is., Rockport, Ont. (W. S. Creighton leg. and Coll.; tentative determination, see under geographic variation in *flavus*). Several collections by A. C. Cole, A. Van Pelt, and myself show that *nearcticus* is fairly common at intermediate elevations in the southern Appalachian mountains of extreme western North Carolina and eastern Tennessee. It has never been taken in the Gulf States, with the single possible exception of an old series marked "Tex." in the USNM. Following are given the westernmost records verified during the present study: Ames, Iowa (W. F. Buren leg.; USNM); Palo Alto Co. and Dickinson Co., Iowa (R. L. King leg. and Coll., MCZ); Deadwood, S. Dak. (E. and G. C. Wheeler leg.; G. C. Wheeler Coll.); Hill City, S. Dak. (W. S. Creighton leg. and Coll.); Devils Tower, Wyo. (Creighton leg. and Coll.).

ECOLOGY. This species is most commonly encountered in dense, moist woodland. Workers and brood are usually found assembled in galleries under rocks and fallen logs, but by digging

to the side away from these shelters, one can easily disclose lateral galleries leading off into the open soil, and workers are often turned up by random trenching through the soil.

A nuptial flight involving both sexes was observed by Dr. Mary Talbot (*in litt.*) at Gibraltar Island, Put-in Bay, Ohio, around 5 p.m. on August 26, 1930. I have verified the following *in nido* records of reproductives: Hull, Que., VIII-13-1913 (MCZ); Kingsmere, Que., IX-1-1913 (MCZ); Woods Hole, Mass., IX-23-1901 (MCZ); Arlington, Mass., VIII-30-1952 (E. O. Wilson leg.; MCZ), VII-17-1953 (W. L. Brown leg.; MCZ); E. S. George Reserve, Mich., VIII-23-1953 (M. Talbot leg. and Coll.); Catawba, Ohio, VIII-18-1938 (M. Amstutz leg.; Talbot Coll.); South Bass Island, Ohio, VIII-15-1931 (Talbot leg. and Coll.); Green Island, Ohio, VIII-25-1932 (Talbot leg. and Coll.); Louisville, Ky., IX-3-1950 (Wilson leg.; MCZ); Palo Alto Co., Iowa, VII-30-1946 (R. L. King leg. and Coll.); Dickinson Co., Iowa, VIII-17-1947 and VIII-17-1952 (King leg. and Coll.).

Lasius talpa Wilson, new species

(Subg. *Cautolasius*)

DIAGNOSIS. An eastern Asian species best distinguished from other members of the subgenus by its very hairy, small-eyed worker caste.

Worker. (1) Monomorphic to feebly polymorphic. Head shape similar to *nearcticus*, subquadrate with widely spaced mandibles.

(2) Eyes very small, usually with only 6-12 ommatidia and a recorded maximum of 17 (Miao T'ai Tze).

(3) Numerous erect hairs on the scape along the plane of count standing out above the combined ground pubescence and subdecumbent to erect hairs of intermediate length. Standing hairs also abundant on the tibiae. Standing body pilosity in general denser than in other *Cautolasius*.

Queen. (1) Best distinguished from other *Cautolasius* species by the presence of numerous standing hairs on the scape.

(2) Possibly averaging smaller than other *Cautolasius* species: three queens from the holotype nest series have HW's of 1.33, 1.35, and 1.35 mm. respectively.

(3) Body uniformly light brown, overall lighter than in other members of the subgenus.

Male. Lacking a dependable pilosity character; at most two or three erect hairs can be seen on the outer femoral surfaces, a condition probably overlapped by *nearcticus.* The mandibles may have a distinctive shape: the one perfect specimen I have examined, from the holotype nest series, had the masticatory border smooth, concave, and terminating in a sharply angular basal corner, which condition has been encountered elsewhere only in the highly variable *flavus* mandible.

HOLOTYPE. A worker in the Okamoto Collection selected from a series collected at Hirooka, Shikoku, on July 23, 1946, with associated queens and males (H. Okamoto leg.). PW 0.54 mm., HW 0.76 mm., SL 0.60 mm., SI 79, ommatidium number 9 and 10. Paranidotype workers, queen, and male in Okamoto Coll. and MCZ.

FURTHER DESCRIPTION. *Worker.* PW range 0.38-0.60 mm.; maximum intranidal PW range 0.38-0.51 mm. (Yasu) and 0.50-0.60 mm. (Hirooka III-8-1936). SI-HW regression zone high, at lower limit of northern Eurasian *flavus* zone (*q.v.*) and below that of *nearcticus.* Dentition similar in variation to that of *flavus* of comparable size; typically two basal teeth and occasionally a third intercalary one; the second intercalary tooth often dropping out. Terminal segments of maxillary palp apparently varying as in *fallax.* The Hirooka III-8-1936 series contains some workers with VI equalling V and some with VI exceeding V, while all of the Yasu workers have VI exceeding V. Petiole always showing some degree of emargination, although this tends to be feeble in small specimens. Cephalic pubescence as dense as in extreme *nearcticus* (see under discussion of geographic variation in *flavus*). Body and appendages uniformly medium yellow.

Male. Parameres and volsellae resembling those of other *Cautolasius.* Subgenital plate subquadrate, with a single prominent posterior setiferous lobe; posterolateral flanges drawn out laterally and very thin and acute.

GEOGRAPHIC VARIATION. Although available series are far too scanty to judge, it may be significant that the workers with the largest eyes are from the westernmost locality, Miao T'ai Tze.

DISTRIBUTION. A limited series, consisting of a total of 45 workers, 3 queens, and 2 males, was examined from the following localities. KYUSHU: Hikosan (Buzen) (2 series, K. Yasumatsu leg. and Coll., MCZ). SHIKOKU: Hirooka (holotype nest series; also III-8-1936, H. Okamoto leg. and Coll., MCZ); Yasu (Okamoto leg. and Coll., MCZ); Kochi (Okamoto leg. and Coll., MCZ). HONSHU: Tokyo, winged queens IX-1931 (L. Gressitt leg.; MCZ); Ichinomiya (F. Silvestri leg.; MCZ); Kanagawa Pref. (H. Sauter leg.; MCZ); Minoo, Osaka Pref. (M. Azuma leg.; Holgersen Coll.); Arima, near Kobe (Azuma leg.; USNM). KOREA: Pyongyang (Keijo) (Silvestri leg.; MCZ), CHINA: Peking (C. F. Wu leg.; MCZ); Miao T'ai Tze, Shensi (W. L. Brown leg.; MCZ).

ECOLOGY. Dr. W. L. Brown has supplied me with field notes on his Chinese collection. Miao T'ai Tze is located in the Tsinling Shan at an elevation of over 6000 feet. The colony was situated in a small rotting stump on a steep slope in moist, mixed fir-hardwood forest (*Liquidambar, Acer,* and bamboos prominent) about 200 feet above the town. A large colony of *L. flavus* was found under a stone about 400 feet higher in a forest clearing. It is conceivable that *talpa* is the ecological equivalent of the North American species *nearcticus* in that it may tend to replace *flavus* in moister, more densely wooded situations.

Lasius fuliginosus (Latreille)

(Subg. *Dendrolasius*)

Formica fuliginosa Latreille, 1798, Essai Fourmis France, p. 36; worker, queen, male; original description. Type locality: France.

Lasius fuliginosus var. *nipponensis* Forel, 1912, Ann. Soc. Ent. Belg., **56:** 339; worker; original description. Type locality: Tokyo. NEW SYNONYMY.

Lasius nipponensis, Santschi, 1941, Mitt. Schweiz. Ent. Ges., **18:** 278.

Lasius fuliginosus var. *orientalis* Karawajew, 1912, Rev. Russ. Ent., **12:** 586–587; worker; original description. Type locality: Korea. NEW SYNONYMY.

Acanthomyops fuliginosus capitatus Kuznetzov-Ugamskij, 1928, "Ants of the Southern Ussuri Region" (In Russian), U. S. S. R. National Geographic Society Publications, p. 18; 4 figs. p. 43: worker; original description. Type locality: Okeanskaja Railroad Station, near Vladivos-

tok, Soviet Maritime Territory, by present restriction. NEW SYN-ONYMY.

Lasius fuliginosus orientalis, Kuznetzov-Ugamskij, 1929, Zool. Anz., **83:** 24. [*nec* Karawajew; objective synonym of *capitatus*, *vide supra*.]

DIAGNOSIS. *Worker*. (1) Head usually deeply concave in full face, the depth of the concavity 0.06 mm. or more except in some series from northeastern Asia (see under geographic variation).

(2) Antennal scapes short-elliptical in cross-section, so that for most of their length the minimum width at any point is 0.8 × the maximum width at that point or greater.

(3) Petiole in frontal view broadest at about the level of the dorsal margin of the anterior foramen, gradually narrowing to the top. The dorsolateral angles broadly and evenly rounded; the dorsal margin narrow, convex to feebly emarginate. In side view the petiole symmetrical, with both faces feebly and evenly convex, tapering together to form a narrow-U-shaped dorsal crest (Pl. 2, Fig. 7).

(4) The hairs of the exposed gastric tergites shorter than in *spathepus* and *crispus*, rarely longer than 0.08 mm. and probably never surpassing the longest hairs of the pronotum. The appendages covered with dense appressed-to-decumbent pubescence but with few or no standing hairs.

Queen. (1) HW 1.41 mm. (Odawara, Japan) to 1.65 mm. (England); see under geographic variation.

(2) Lacking the "beta" characteristics of the *spathepus* queen, i.e. the occipital margin in full face is only weakly concave, the head is about as long as broad or longer, and the mandibles are not exceptionally reduced relative to the remainder of the head.

(3) The entire body, exclusive of the appendages and (in European series) the anterior half of the head, covered with abundant, coarse suberect-erect hairs. In occasional specimens these hairs are rather sparse on the gastrict tergites, but this may be due to wear. The entire body is covered with appressed ground pubescence of varying density which partly obscures the smooth, shining cuticular surface.

(4) Petiolar lateral outline as in worker. Frontal outline typically as in worker and dorsal margin showing same degree

of variation as in that caste; occasionally the broadest level is well above its usual location at the dorsal margin of the anterior foramen.

(5) Median clypeal carina feebly developed (see under *buccatus*).

Male. (1) HW 1.00 mm. (Kiev) to 1.24 mm. (Innsbruck).

(2) Scape short-elliptical to circular in cross-section.

(3) Petiolar outline in side view similar to that of the worker, differing only in being generally thicker. In frontal view the broadest point is at the level of the dorsal margin of the anterior foramen or higher; the dorsal margin is convex in all series examined.

(4) Pygostyle similar to that typifying the subgenus *Lasius:* thumb-shaped, nearly as broad near the tip as at the basal attachment (Pl. 2, Fig. 11). The usual form of the subgenital plate is shown in Plate 2, Fig. 9.

GEOGRAPHIC VARIATION. *The Odawara queens.* The single series of Asiatic *fuliginosus* queens (Odawara, Honshu; M. Kubota leg.; MCZ) I have been able to examine shows several differences from European material that may reflect geographic variation. These queens are smaller, ranging 1.45-1.48 mm. in HW as opposed to 1.62-1.70 mm. for the European series. They have more abundant standing hairs on the anterior half of the head, so that in full face suberect-erect hairs are abundant along the genal outline from the anterior border of the eye to the mandibular insertion, whereas in European material hairs are rare or absent there. The appressed ground pubescence of the body is far denser in the Odawara queens, giving a grey overtone to the body surface at low magnifications. A case may be made in the future for according this form specific status; at present such a move seems inadvisable in view of the fact that the Odawara form is completely allopatric and the associated workers and males are hardly separable by themselves from the typical *fuliginosus.*

Worker petiolar pilosity. In European series the longest erect hairs of the dorsal petiolar margin are consistently shorter than one-half the maximum width of the scape, whereas in Japanese series they are usually longer than one-half. Series from the following Asiatic localities were found however to be closer to the European type: Tokyo (MCZ); Ashoromura, Hokkaido

(Yasumatsu Coll.); Kongosan, Korea (Yasumatsu Coll.); Miao T'ai Tze, Shensi, China (W. L. Brown leg.; MCZ); Harbin, Manchuria (Yasumatsu Coll.); Okeanskaja, Siberia ("*capitatus*" syntypes).

Worker occipital outline. Series from northeastern Asia (Ashoromura, Kongosan, Miao T'ai Tze, Harbin, Okeanskaja) have unusually shallow occipital emarginations (viewed in perfect full face, the emargination 0.03 mm. deep or less). This condition occurred in only 7 out of 47 European nest series examined.

DISTRIBUTION. This species is widely distributed in the Palaearctic Region. It occurs in Ireland (O'Rourke, 1950), in England north to Lancashire and Yorkshire (Donisthorpe, 1927), in Norway north to Elverum and west to Søndeled and Lyngør (Holgersen, 1944), and in several localities in southern Sweden (Forsslund, 1947). I have determined specimens from Kuopio, southern Finland (O. Wellenius leg.; MCZ). Extensive collections studied during the course of the present work combine with the independent statements of many authors in a massive European literature to give the impression that *fuliginosus* is a common species throughout northern Europe. In the west it extends as far south as Centellas, Barcelona (de Xaxars leg.; MCZ), but has never been taken in North Africa, the Balearics, or the Canaries. In the east it is widespread in northern Italy and northwestern Yugoslavia (numerous series mostly in the MCZ) and extends through the mountains of central Yugoslavia (Zimmermann, 1934) to as far south as Mali Daiti and Tirana in Albania (Ravasini and Lona leg.; MCZ). I have seen a single series labelled "Syrien Libanon" (E. V. Bodemeyer leg.; Holgersen Coll.); the species is probably rare or local in this area since it was not in the substantial collection of the genus made by Dr. K. Christiansen in the mountains of Lebanon. Karawajew (1926) records it from the Krimea. It is apparently rare or absent in Central Asia (Menozzi, 1939; Eidmann, 1941). Bingham (1903) records it from Thana, near Bombay, but this is a rather incredible record, in the same class as a single specimen now in the MCZ labelled "Tutu River, North Borneo." Some records from eastern Asia have already been given in the section on geographic variation. Additional records accumulated during the present study include the following: Mt. Rokko and Yamashita, Hyogo Pref., Honshu (M. Azuma leg.; USNM); Mt.

Kajigamori, Shikoku (H. Okamoto leg. and Coll., MCZ); Kochi, Shikoku (Okamoto leg. and Coll.); central Korea, no further data (K. Yasumatsu Coll., MCZ).

ECOLOGY. Many European observers have reported independently on various aspects of the ecology of this ant, and together they present a reassuringly consistent picture. *Fuliginosus* nests primarily in standing tree trunks and rotting stumps, and only occasionally in and around the roots of trees, under stones, and in open soil. In a random field survey in Germany, Gösswald (1932) recorded 63 nests in wood, 2 under stones, and 5 in open soil. He found the species nesting most commonly in old poplars and willows in dry meadows. It is often locally abundant; O'Rourke (1950) notes that in Ireland it may become the dominant ant in oak woods.

Fuliginosus almost invariably constructs a carton nest. The composition of the carton has been analyzed by Stumper (1950), who finds that it consists primarily of macerated wood hardened with secretions from the mandibular glands. There may be some soil particles mixed in, especially in subterranean nests, but these constitute a very minor fraction. Stumper was unable to find supporting evidence for the old contention that several species of symbiotic fungi are normally grown in the carton walls.

Fuliginosus forages during both the day and night, forming long, conspicuous columns which usually lead to trees infested with aphids or coccids; the excreta of these latter insects forms a principal food source for the ant. In addition, many authors have observed workers carrying dead or crippled insects back to the nests.

Eidmann (1943) has studied overwintering in this species. A colony which he kept under observation through the autumn moved from a position in a tree bole to subterranean quarters directly beneath the tree. The winter carton nest had chambers twice the size of those in the summer nest, and its walls were conspicuously studded with grains of sand. Medium-sized and full grown larvae were found hibernating with the adults.

Winged reproductives have been taken in the nests from May to September. The nuptial flights apparently take place earlier than in other members of the genus; literature records span the period May 4 to July 27. The flights occur mostly in the afternoon, although some authors, such as Escherich and Ludwig

(1906), have suggested that they occur at night also. According to Donisthorpe (1927), the mating behavior shows early signs of parasitic degeneration. There is a marked decrease in the size difference between the two sexes, and the nuptial flight appears to have been partly suppressed. In one case Donisthorpe observed nestmates copulating on vegetation in the immediate vicinity of the parent nest.

Donisthorpe (1922) has also reviewed the extensive literature on colony founding in this species. It has been proven without any doubt to be a temporary social parasite on *Lasius umbratus* (= *mixtus*), which species was defined in the old sense and may well include *L. rabaudi* also. Numerous mixed colonies have been found in nature, and successful adoptions of dealate queens by host colonies have been repeatedly obtained under artificial conditions. This habit places *fuliginosus* in the extraordinary position of being a social hyperparasite, since *umbratus* is parasitic itself on members of the subgenus *Lasius*. In more recent years, Stärcke (1944) has obtained the experimental adoption of *fuliginosus* queens by colonies of *L. rabaudi* (= *meridionalis*), *L. niger*, and *L. alienus*.

SYNONYMY. *Lasius fuliginosus* var. *nipponensis* Forel. Lectotype by present selection, a worker in the Forel collection. Head and thorax partly crushed and not measurable. Pilosity of petiolar dorsal margin long, characteristic of the Japanese population already described.

Lasius fuliginosus var. *orientalis* Karawajew. Since the types are not available, synonymy in this case is tentative. The differences stated in the original description are of a trivial nature, and it would seem that if Karawajew had really had *spathepus* before him instead of *fuliginosus*, he would have noticed at least one of the several excellent characters which separate workers of these two species.

Acanthomyops fuliginosus capitatus Kuznetzov-Ugamskij. Lectotype by present selection, a worker in the MCZ labelled "Acanthomyops fuliginosus orientalis Karav. (=capitatus K.)/Far East. Station Okeanskaja, near Vladivostok." PW 0.78 mm. Possessing a shallow occipital emargination and short petiolar hairs, both of which characters seem to predominate in northeastern Asia. Kuznetzov-Ugamskij (1929a) later used Karawajew's name *orientalis* instead of *capitatus*, without disclosing

his reasons for creating the synonymy. If trinomens are to be used at all for this population, it will first have to be ascertained whether the types of the two forms share the same pilosity and cephalic outline characters.

Lasius crispus Wilson, new species

(Subg. *Dendrolasius*)

DIAGNOSIS. An eastern Asian species most readily distinguished by the aberrant pilosity and pubescence of the queen caste.

Queen. (1) Body and appendage hairs much finer than in *fuliginosus,* many curved at the tip or even sinuate. On the appendages, where the pilosity is predominantly decumbent to subdecumbent, the hairs are frequently wicket-shaped in addition, recurving to touch the cuticular surface with their tips.

(2) Body pubescence very sparse or absent, so that the entire cuticular surface is moderately to strongly shining. The appendages are densely covered with appressed hair, the legs somewhat more so than the scapes.

(3) Viewed from the side the crest of the petiole thin and acute; the entire posterior margin of the petiole feebly concave in each of the three specimens examined.

(4) Viewed in full face the genal margins nearly straight, curving inward only near the mandibular insertions. As a result the occipital region appears proportionately wider, and the entire head more sagittate, than in *fuliginosus.*

(5) The median clypeal keel, which is feebly developed in *fuliginosus,* is completely lacking in *crispus.*

Worker. Two workers from Ueda, Honshu, and a small series from central Korea are tentatively and with great reservation placed in this species and used for the following diagnosis.

(1) The standing hairs of the second and third gastric tergites, anterior to the extreme posterior strips, as long as those of the pronotum or longer. In the Ueda series but not in the Korean series, femora with numerous outstanding decumbent to suberect hairs. Cephalic and gastric pilosity denser than in *fuliginosus.*

(2) Petiolar crest viewed from the side thinner and sharper than in *fuliginosus,* the anterior and posterior faces less convex (Pl. 2, Fig. 8).

Male. (1) In side view the anterior and posterior faces of the petiole taper equally to form a narrow, sharp crest. Otherwise very similar to *fuliginosus.*

(2) Terminal segments of maxillary palp highly variable in length as in other *Dendrolasius,* but showing no sign of ankylosis.

(3) Pygostyle and subgenital plate as in *fuliginosus.*

HOLOTYPE. An alate queen collected at Katsura-hama, Shikoku, on August 7, 1940 (H. Okamoto leg. and Coll.). HW 1.48 mm. An identical paratopotype queen is in the MCZ. These two specimens and the Kochi queen have a more extreme pilosity than the Ueda queen; virtually every hair shows curving to some degree, and many of the longer body hairs are sinuate.

FURTHER DESCRIPTION. *Queen.* HW of paratopotype 1.58 mm., of Ueda queen 1.55 mm., of Kochi City queen 1.52 mm.

Worker. PW of Ueda workers 0.64 and 0.72 mm., of Korean series 0.77-0.87 mm.

Male. HW of paratopotype male 1.08 mm., of Ueda series 1.04-1.26 mm. Genitalia identical to that of *fuliginosus.*

DISTRIBUTION. SHIKOKU: Katsura-hama, 2 winged queens and a male; Kochi, a winged queen, IX-5-1935 (H. Okamoto leg. and Coll.). HONSHU: Ueda, a winged queen and 11 males, VI-1934; 2 workers, VI-6-1936 (S. Miyamoto leg.; Yasumatsu Coll. and MCZ). KOREA: ''central Korea'', many workers (Yasumatsu Coll. and MCZ).

Lasius buccatus Stärcke

(Subg. *Dendrolasius*)

Lasius buccatus **Stärcke, 1942, Tijdschr. Ent., 85: 27–28, figs. 6, 7; queen, male; original description. Type locality: Dragocaj-Sarajevo, Bosnia.**

DIAGNOSIS. I have not been able to examine the types, but from Stärcke's figures and description this appears to me to be a good species separated from *fuliginosus* by several cephalic characters in the queen and male.

Queen. (1) A sharp median carina runs from the junction of the clypeus and the frontal triangle to a small shallow pit in the center of the clypeus. The *fuliginosus* clypeus invariably has an indistinct, obtuse median keel running most of its length, but I have never seen the posterior segment prominently de-

veloped. This keel in *fuliginosus* often dips slightly in the middle, and in one series, from Imer, Venezia Tridentina (MCZ), the dip is even developed into a shallow, very indistinct depression, which nonetheless still does not approach the condition figured by Stärcke for *buccatus*.

(2) The head of *buccatus* is narrower than in *fuliginosus*, according to Stärcke about 1.03 × longer than broad (HL/HW). In none of the *fuliginosus* series I have measured does the HL exceed 0.95 × the HW.

(3) Head narrower than the thorax. No specific measurements are given by Stärcke, but if true, this character represents an extraordinary exception to the rule for *Dendrolasius*.

(4) The antenna dark brown, nearly the same color as the head. *Fuliginosus* has medium brown antennae which contrast against the blackish brown head.

Male. (1) Lateral margins of the head, especially the genal margins, more convex than in *fuliginosus*. From Stärcke's figure, the head width just below the eyes is nearly the same as that above the eyes; in *fuliginosus* it is only about 0.9 × as great. As a result the *buccatus* head presents an almost circular outline in frontal view.

(2) Mandibles with seven well developed teeth including the apical. In the single male the dental pattern is the same on both mandibles: the fifth tooth and seventh tooth (the latter on the basal angle) are reduced in size. In *fuliginosus* adventitious denticles are often developed at random along the masticatory border but they are never as large and seldom as numerous as the teeth depicted by Stärcke for *buccatus*, and they never form a constant pattern.

Lasius teranishii Wheeler

(Subg. *Dendrolasius*)

Lasius teranishii Wheeler, 1928, Boll. Lab. Zool. Portici, **21**: 120; queen; *nom. pro Lasius umbratus*, Teranishi, 1927 [*nec* Nylander]. Type locality: Nokkeuchi, Hokkaido.

Lasius umbratus, Teranishi, 1927, Zool. Mag., **39**: 90, 92–93, figs. 6, 6A. Reprinted in "Works of Cho Teranishi, Memorial Volume," 1940, pp. 51, 53–54. [*nec* Nylander.]

Lasius ouchii Teranishi, 1940, "Works of Cho Teranishi, Memorial Volume,"

posthumously published section, p. 76; queen. NEW SYNONYMY (objective synonym of *L. teranishii* Wheeler).

DIAGNOSIS. It is clear from Teranishii's figures that the holotype and single known specimen of this species is not a *Chthonolasius,* as previously considered, but a *Dendrolasius* intermediate in habitus between the "alpha" — form queen of *fuliginosus* and the extreme "beta" — form queen of *spathepus.* Its membership in this subgenus is suggested by the prominent anterior curve of the scutum overhanging the pronotum, by the thickened profile of the petiolar scale, by the more cordate head shape, and by the blackish brown body coloration. It resembles *spathepus* in possessing conspicuously flattened scapes, femora, tibiae, and metatarsi, and in lacking standing hairs on the body. It differs markedly from that species in having an "alpha" head shape, closely resembling that of *fuliginosus.* Also, Teranishi makes no mention of the presence of any aberrant appendage pilosity of the type found in *spathepus.* The petiolar scale is symmetrical in profile, with an evenly rounded dorsal crest, a condition shared with *fuliginosus.*

Lasius spathepus Wheeler
(Subg. *Dendrolasius*)

Lasius spathepus Wheeler, 1910, Biol. Bull., **19**: 130–131, fig.; queen; original description. Type locality: none specified, by inference Nishigahara, near Tokyo.

Lasius fuliginosus var. *spathepus,* Teranishi, 1927, Zool. Mag., **39**: 50.

Lasius spathepus, Wheeler, 1928, Boll. Lab. Zool. Portici, **21**: 121.

DIAGNOSIS. A Japanese and Korean species marked by several excellent characters in all three castes but best distinguished by the aberrant, "beta"-form queen.

Worker. (1) Head broader, occiput usually less concave, and scapes shorter relative to head width than in other *Dendrolasius.*

(2) Antennal scapes flattened to the extent that for most of their length the minimum measurable width at any point is less than half the maximum measurable width at the same point. Tibiae and metatarsi also noticeably flattened.

(3) Hairs of scapes and legs sparser and longer than in other *Dendrolasius.* The standing hairs seen in relief when the hind

tibia is viewed in the plane of its minimum width are often half as long as the greatest width measurement obtained along the length of the tibia in this view, or longer. Tibial hairs appressed to suberect, the majority tending to decumbent.

(4) The petiole seen in frontal view subrectangular; the dorsal border always emarginate to some degree. In side view the anterior face curving back abruptly just above the level of the spiracle, in contrast to the posterior face, which is gently and evenly convex from the posterior foramen to the crest (Pl. 2, Fig. 6).

(5) Propodeum viewed from the side typically higher and more prominent relative to the thorax than in other *Dendrolasius.* A single series from Nanzan, Korea, represents an extreme deviant from this character and is well within the range of variation of *fuliginosus.*

Queen. (1) Averaging and ranging larger than other *Dendrolasius;* HW 1.96-2.03 mm.

(2) Head much broader than long, with a deeply emarginate occipital border and strongly convex sides which curve in sharply at the mandibular insertions. The mandibles exceptionally small relative to the head.

(3) Scapes, femora, tibiae, and metatarsi greatly flattened, the minimum width of the scape at midpoint about half the maximum width.

(4) The broad surfaces of the scape coarsely and evenly punctate.

(5) The dorsal border of the petiole emarginate for nearly its entire extent. In side view the scale is anteriorly truncated as in the worker.

(6) The scapes, tibiae, and metatarsi densely covered with long, predominantly suberect, coarse, silvery yellow hairs. On the tibiae and metatarsi these form two layers, those in the lower, short and densely packed and those in the upper, long, curved and sparse.

(7) Ground pubescence completely lacking on the body. Hairs are limited mostly to the mandibles, clypeus, gula, posterior third of the head, petiole, anterior first gastric tergital surface and posterior gastric tergital margins. The alitrunk is completely lacking in pilosity of any kind except for a few scattered short hairs on the propodeum.

(8) The body is very feebly sculptured and strongly shining, except for the petiole and anterior clypeal margin, which are shagreened; and the mandibles, which are longitudinally striate.

(9) Median clypeal carina well developed posteriorly but vanishing in the planed, shagreened anterior fourth of the clypeus.

Male. (1) Averaging and ranging larger than other *Dendrolasius;* HW 1.13-1.27 mm.

(2) Scapes and tibiae distinctly flattened.

(3) Petiole in frontal view distinctly emarginate and much broader than in other *Dendrolasius.* Petiolar outline in side view similar to that described for the worker.

(4) Pygostyle as in *Chthonolasius,* i.e. thicker than in *Lasius s. s.* and tapering gradually from base to tip (Pl. 2, Fig. 12). The subgenital plate distinctive in shape: the posterior margins between the setiferous lobes and posterior angles more deeply convex than in *fuliginosus* and *crispus,* causing the setiferous lobes to project back more prominently (Pl. 2, Fig. 10).

(5) Scape and tibial pilosity longer and sparser than in other *Dendrolasius.*

HOLOTYPE. A queen in the MCZ labelled ''Japan. Kuwana Coll. 1910.'' HW 2.03 mm.

DISTRIBUTION. Following are all of the records verified during the present study. HONSHU: Kanagawa Pref. (H. Sauter leg.; MCZ); Kamakura, Kanagawa Pref. (F. Silvestri leg.; MCZ); Odawara, Kanagawa Pref., winged queens and males VI-22-1952 (M. Kubota leg.; MCZ); Yokohama (L. Gressitt leg.; MCZ); Tokyo (Gressitt leg.; MCZ); Ueda (S. Miyamoto leg.; Yasumatsu Coll.); Hiroshima (Miyamoto leg.; Yasumatsu Coll.). SHIKOKU: Mt. Kajigamori (H. Okamoto leg. and Coll.). KYUSHU: Kubotayama (Yasumatsu Coll.); Hikosan (Yasumatsu leg. and Coll.); Sobosan (Fujino and Yasumatsu leg.; Yasumatsu Coll.); Magari-fuchi (Hori and Fujino leg.; Yasumatsu Coll.); Fukuoka (Shirozu leg.; Yasumatsu Coll.). KOREA: Seoul (Yasumatsu Coll. and MCZ); Mt. Kangaku, near Seoul (K. S. Ryu leg.; Yasumatsu Coll.); ''Nanzan'' (Shirozu leg.; Yasumatsu Coll.); Mt. Kongo (Shirozu leg.; Yasumatsu Coll.).

SYNONYMY. Wheeler (1928) was wrong in considering Forel's *L. fuliginosus* var. *nipponensis* a synonym of *spathepus.*

The *spathepus* queen does not represent, as he supposed, the "beta" form of a *fuliginosus*-like species. Rather *spathepus* and *fuliginosus* occur together in Japan as distinct species and are separated by excellent characters in all three castes.

[Lasius nemorivagus Wheeler]

(Subg. *Chthonolasius*?)

Lasius nemorivagus Wheeler, 1914, Schrift. Phys.-ökon. Ges. Königsberg, **55:** 123; queen; original description (Baltic amber).

DIAGNOSIS. *Queen.* According to Wheeler, maxillary palps typical for the subgenus *Lasius,* but head broader than thorax, a *Chthonolasius* and *Dendrolasius* character. Funicular joints II-VI broader than long, VII-X as broad as long. Body more thickset, appendages stouter than in *schiefferdeckeri.* Size small, total length 6 mm., the lower limit later given by Wheeler (1917a) for the queen caste of "*neoniger*" (*sitkaensis, niger,* and *neoniger*). Body with sparse erect hairs; appendages presumably bare.

HOLOTYPE. The single type specimen was probably lost with the rest of the Königsberg Geological Institute Collection during the Second World War.

Lasius umbratus (Nylander)

(Subg. *Chthonolasius*)

Formica umbrata Nylander, 1846, Acta. Soc. Sci. Fenn., **2:** 1048–1050; queen, male; original description. Type locality: Helsinki, by selection of Stärcke (ref. below).

Formica mixta Nylander, 1846, *ibid.,* pp. 1050–1052; queen; original description. Type locality: Upsala. NEW SYNONYMY.

Lasius umbratus mixtus, Forel, 1874, Les Fourmis de la Suisse (Nouv. Mem. Soc. Helv. Sci. Nat.), p. 47.

Formica affinis Schenck, 1852, Jahrb. Ver. Nat. Nassau, **8:** 62–63; worker, queen, male; original description. Type locality: Weilburg, Nassau, Germany, by present selection. NEW SYNONYMY.

Lasius umbratus affinis, Forel, 1874, *loc. cit.*

Formica aphidicola Walsh, 1862, Proc. Ent. Soc. Phila., **1:** 310; worker, male; original description. Type locality: Rock Island, Illinois, by virtual designation. NEW SYNONYMY.

Lasius umbratus mixtus var. *aphidicola*, Emery, 1893, Zool. Jahrb. Syst., **7:** 640.

Lasius umbratus aphidicola, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 425.

Lasius umbratus var. *mixto-umbratus* Forel, 1874, *op. cit.*, p. 48; worker; original description. Type locality: by inference, Switzerland. NEW SYNONYMY.

Lasius umbratus var. *exacutus* Ruzsky, 1904, Kasan Univ. Obschchestvo estestvoispytatelei Protokoly Zasiedanii, no. 206, p. 15; worker; original description (in Russian). Type locality: Caucasus, 8000 feet. NEW SYNONYMY.

Lasius umbratus var. *mixto-affinis* Ruzsky, 1904, *loc. cit. Nomen nudum.*

Lasius umbratus var. *mixto-bicornis* Ruzsky, 1905, "Formicariae Imperii Rossici," Schrift. Naturforsch.-Ges. Univ. Kasan, **38:** 292. *Nomen nudum.*

Lasius umbratus var. *affino-umbratus* Donisthorpe, 1914, Ent. Rec., **26:** 40; worker; original description. Type locality: Tenby, England. NEW SYNONYMY.

Lasius umbratus var. *przewalskii* Ruzsky, 1915, Ann. Mus. Zool. Acad. Sci. Petrograd (Academii Nauk S. S. S. R., Leningrad, Zoologischeskii muzei), **20:** 434; worker; original description (in Russian). Type locality: Valley of River Tetunga, northeastern Tibet. NEW SYNONYMY.

Lasius umbratus exacutus var. *prczewalski* [!], Emery, 1924, Gen. Insect. (Wytsman), Fasc. **183:** p. 234.

Lasius bicornis exacuta var. *prezcwalskii* [!], Menozzi, 1939, Atti Soc. Ital. Sci. Nat., **78:** 32.

Formicina umbrata distinguenda Emery, 1916, Rend. Acc. Bologna, pp. 64–65; worker, queen; original description. Type locality: Bologna. NEW SYNONYMY.

Formicina umbrata var. *hybrida* Emery, 1916, *ibid.*, p. 66. Synonymy by Stärcke, 1937, Tijdschr. Ent., **80:** 57.

Formicina umbrata var. *nuda* Bondroit, 1917, Bull. Soc. Ent. Fr., **86:** 176. Synonymy by Stärcke, *op. cit.*, p. 56.

Formicina umbrata var. *sabularum* Bondroit, 1918, *op. cit.*, **87:** 31. Synonymy by Stärcke, *op. cit.*, p. 56.

Formicina belgarum Bondroit, 1918, *op. cit.*, **87:** 31; worker, queen; original description. Type locality: none designated. NEW SYNONYMY.

Lasius umbratus var. *belgarum*, Stärcke, 1937, *op. cit.*, **80:** 57.

Lasius bicornis var. *citrina* Emery, 1922, Bull. Soc. Ent. Ital., **54:** 12; worker; original description. Type locality: Monte Gargano, Puglia, Italy, by present restriction. NEW SYNONYMY.

Lasius umbratus var. *viehmeyeri* Emery, 1922, *ibid.*, pp. 13–15, fig. 2;

worker, queen; original description. Type locality: Erymanthos, Peloponnesus, Greece. NEW SYNONYMY.

Lasius viehmeyeri, Stärcke, 1937, *op. cit.*, **80:** 53.

Lasius silvestrii Wheeler, 1928, Boll. Lab. Zool. Portici, **20:** 120–121; queen; original description. Type locality: Mt. Maya, nr. Kobe, Honshu. NEW SYNONYMY.

Lasius viehmeyeri var. *dalmatica* Stärcke, 1937, Tijdschr. Ent., **80:** 53–54; queen; original description. Type locality: Knin, near Zara, Yugoslavia. NEW SYNONYMY.

Lasius umbratus var. *hirtiscapus* Stärcke, 1937, *ibid.*, p. 43; queen; original description. Type locality: ''Kiczera,'' Beskids, Czechoslovakia. NEW SYNONYMY.

Lasius umbratus distinguendus var. *cereomicans* Stärcke, 1937, *ibid.*, pp. 48–49; worker, queen, male; original description. Type locality: Aosta, Piemonte, Italy. NEW SYNONYMY.

Lasius silvestri [!] var. *osakana* Santschi, 1941, Mitt. Schweiz. Ent. Ges., **18:** 278; queen; original description. Type locality: Ikeda, Osaka Pref., Honshu. NEW SYNONYMY.

Chtonolasius [!] *affinis* var. *nyárádi* Röszler, 1943; Zool. Anz., **144:** 47–48; worker, queen; original description. Type locality: Nyárádtö, Rumania. NEW SYNONYMY.

Lasius umbratus epinotalis Buren, 1944, Iowa State Coll. Jour. Sci., **18:** 297–298; worker; original description. Type locality: Bellevue, Iowa. NEW SYNONYMY.

Lasius subumbratus epinotalis, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 424.

DIAGNOSIS. *Queen.* (1) Most of the body surface covered with abundant, relatively short, silvery yellow, predominantly erect hairs. The hairs on the first three gastric tergites with maximum length variable internidally, 0.05-0.11 mm., never more than one-half the maximum width of the hind tibiae at midlength, and often less than one-third; very variable in density, never less than 20 hairs visible above the dorsal profile of the first gastric segment seen in perfect side view and usually more than 30, but never dense enough to overlap one another extensively. Erect hairs forming a fringe on the dorsal crest of the petiole, their maximum length close to that of the gastric hairs. The longest hairs of the alitrunk are on the scutellum, maximum length 0.12-0.21 mm. Maximum length of scutal hairs 0.05-0.15 mm. (see also under geographic variation). Maximum length of cephalic hairs exclusive of those on the clypeus 0.09-

0.11 mm. Body hairs mostly straight or feebly curved, rarely strongly curved (on propodeum) and never sinuate. Standing hairs may or may not be present on the appendages (see also under geographic variation). All of body and appendages densely covered with short, whitish pubescence which is completely appressed on the body and appressed to decumbent on the appendages; on the gaster it is often abundant enough to obscure partly the shining cuticular surface and to present a whitish overcast to the naked eye.

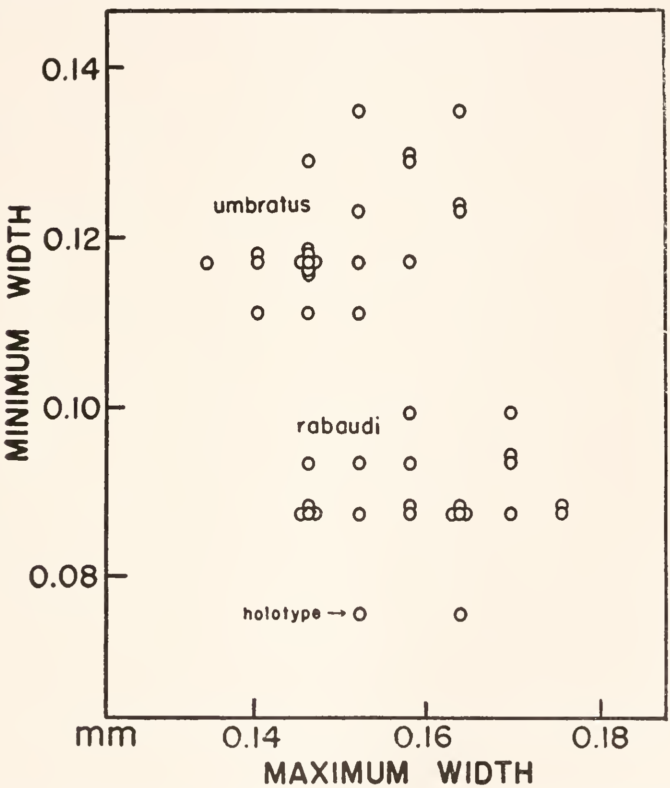


Fig. 15. Flattening of the scape in the queen caste of the two Palaearctic sibling species *L. umbratus* and *L. rabaudi.* This is the principal character separating the two species. Further explanation in the text. Nest series chosen at random; no more than two queens per series were measured.

(2) HW ranging 1.40-1.82 mm. in 45 nest series measured (see also under geographic variation). SI of size extremes 75 and 81.

(3) Petiole in frontal view tapering gradually but distinctly from the level of maximum width (just above the foramina) to the dorsal crest, the width just ventral to the dorsolateral angles 0.9 × the maximum width or less but the frontal outline rarely subquadrate as in *rabaudi.* Dorsal crest extremely variable in shape, from very feebly concave or even straight to deeply concave with the emargination almost right-angular. The dorsolateral angles always broadly rounded. In side view the scale is narrow and with an acute dorsal crest.

(4) The scape short-elliptical to circular in cross-section, never conspicuously flattened, the minimum width at the midpoint 0.11 mm. or greater (Fig. 15). The third funicular segment 1.0-1.5 × longer than broad.

(5) Body medium to dark brown, the appendages lighter, light to medium brown.

Worker. (1) Pilosity and pubescence as in queen. Maximum length of hairs of first gastric tergite anterior to the extreme posterior strip 0.06-0.08 mm., not exceeding one-half the maximum width of the hind tibia at midlength. Alitruncal and cephalic hairs with maximum length of about 0.11 mm.

(2) Petiole in frontal view tapering slightly from the widest point, just above the foramina, to the dorsal crest. The dorsal crest broad and very variable in outline, from flat or even feebly convex to deeply concave; the emargination rounded or angular, never as deep as in *bicornis,* i.e. the width (taken at the midpoint of the depth measurement) always exceeds the depth. Intranidal variation considerable; the petiole in a single series may range from flat to distinctly emarginate. In side view the scale is relatively narrow, its dorsal crest acute.

Male. (1) Pilosity and pubescence essentially the same as in the queen and worker, except that hairs of the first three gastric tergites are more frequently subdecumbent-suberect. Despite this greater tendency toward obliqueness, the hairs of the first gastric tergite are still too sparse to show much overlap, and their maximum length (excluding those on the extreme posterior strips) ranges internidally 0.07-0.08 mm., or always less than 0.7 × the maximum width of the hind tibia at its midlength.

Maximum length of scutellar and cephalic hairs (excluding those on the clypeus) 0.09 mm.

(2) HW 0.85-1.23 mm. in 15 nest series measured; SI of the extremes 62 and 66.

(3) Petiole in frontal view tapering dorsally as in queen and worker. Dorsal margin flat to deeply emarginate, the emargination rounded or angular, never greater than semicircular or right-angular. The scale in side view relatively thin, with an acute dorsal crest.

LECTOTYPE. A dealate queen in the Helsinki Museum, selection by Stärcke (1937). From Stärcke's description it is clear that this specimen is large (head width across and including eyes 1.71 mm.) and at one extreme of the normal allometric variation in head shape, pilosity, etc. (see section below).

GEOGRAPHIC VARIATION. *Size and correlated allometric characters in the queen.* Allometric variation in several diverse characters is quite extensive and complicated in the European population of *umbratus*. This has been the principal origin of the ponderous and almost hopelessly confusing mass of synonymous specific, subspecific and varietal names that have been piled around *umbratus* in past years. The single most important synonym of *umbratus* is the "species" *mixtus* which, as will be shown below, rests at one extreme of allometric variation opposite the "typical" *umbratus*. When *mixtus* falls into synonymy, most of the other satellite forms of *umbratus* fall with it, since these have been erected on the kind of characters which are supposed to be of species value in distinguishing *mixtus*.

According to Stärcke (1937), the *mixtus* holotype differs from the *umbratus* lectotype in the following characters: (1) small size (HW across and including eyes 1.50 mm.), (2) occipital border less concave, (3) pubescence denser, (4) puncturation of the head finer, so that at a magnification of 70× the interstices are at least twice as wide as the punctures themselves (in the *umbratus* lectotype the cephalic sculpture consists of saucer-shaped depressions much wider than the interstices), (5) tibiae bare of pilosity, head with sparse pilosity (erect hairs abundant on tibiae of *umbratus* lectotype), (6) penultimate funicular segment (no. 10) broader than long (longer than broad in the *umbratus* lectotype). To these queen characters we can add the one often advanced as diagnostic for the worker caste: standing

hairs present on the scape and tibiae in *umbratus*, absent in *mixtus*. According to Stärcke, *mixtus* workers are characterized by an absence of pilosity in the center of the head, combined with a sinuate to flat dorsal petiolar crest; *umbratus* has "appreciable" pilosity in the center of the head, combined with a more deeply emarginate dorsal petiolar crest. Stärcke abandons

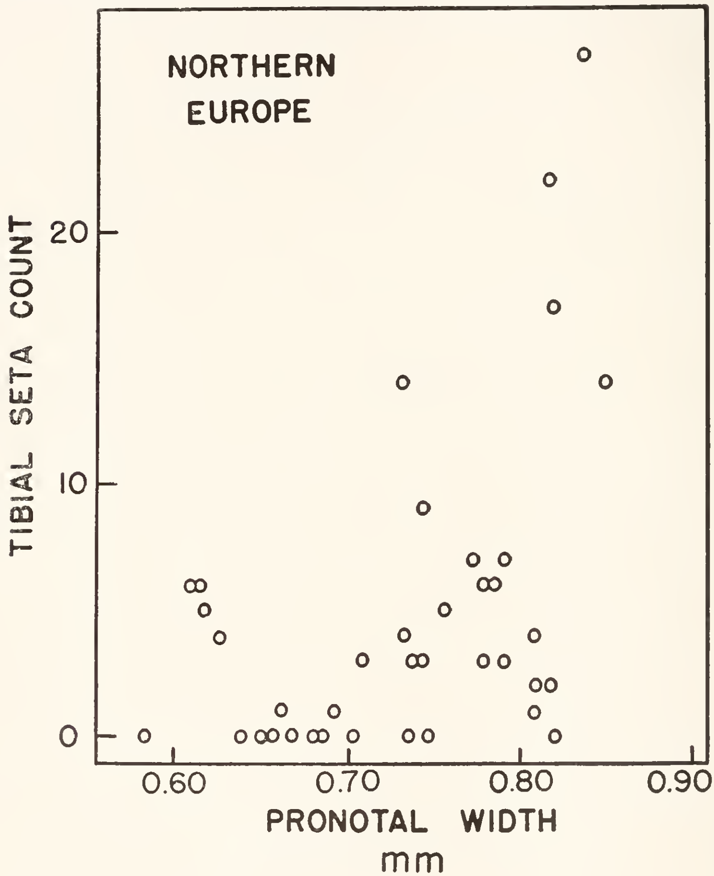


Fig. 16. Pronotal width-tibial seta count relationship in a random northern European sample of *L. umbratus* workers. Nest series chosen at random; no more than two workers per series were measured.

the appendage pilosity character, since he considers that a southern race of *umbratus* (*distinguendus* Emery) lacks the diagnostic standing hairs and must be separated in other ways.

During the present study I have been fortunate in being able to study large numbers of series of *umbratus* from all over Europe and North Africa, including peripheral areas in Spain, Algeria, Lebanon, European Russia, Finland, Scandinavia, and England. Over 40 of the series contained queens. As a result I now feel reasonably confident in saying that each of the characters listed above for both female castes grades through evenly from the "*umbratus*" extreme to the "*mixtus*" extreme and that no single character, or combination of characters, can be used to separate *umbratus* and *mixtus* as species.

Furthermore, all of these characters except pubescence show some degree of correlation with total body size and with each other. In other words, they appear to be simply pleiotropic expressions of a single strong allometric trend. Specifically, as size increases, the occipital concavity deepens, the cephalic punctures broaden and the body surface grows more opaque, the standing hairs on the body and appendages grow proportionately denser, and the funicular segments elongate. Pubescence alone varies erratically and independently of the other characters.

The amount of size variation and the degree of expression of the pilosity character (its regression slope), are in turn subject to geographic variation. In general, queens from southern areas (Spain, Italy, Yugoslavia, Lebanon) are less size variable and fail to develop standing tibial pilosity with increase in size. The maximum HW range ascertained for the southern population as a unit was 1.64-1.82 mm., while that of the northern population was 1.49-1.80 mm. In both cases there is an unexpected skewness toward the smaller size classes. The northern queens begin to develop standing hairs on the scapes and tibiae above a HW of about 1.60 mm., and the largest individuals have dense standing pilosity on the scape (Stärcke's var. *hirtiscapus*). Thus, the northern population shows extensive variation, from the smallest "*mixtus*" individuals up to the largest, hairy forms. The southern population, on the other hand, exhibits only the upper half of the size variation shown by the northern population, thereby missing the "*mixtus*" form, and in addition the largest

individuals do not develop standing hairs on the scapes as do northern queens of comparable size.

There are therefore only two real detectable differences between the extreme northern and southern European samples: (1) the southern sample apparently lacks the lower segment of the size range exhibited by the northern sample; (2) queens above 1.60 mm. develop standing hairs in the northern but not in the southern sample. Contrary to Stärcke's statement, I have been unable to find any difference between the northern and southern populations in the length of scutal and cephalic hairs.

Numerous North American series examined ranged in HW from 1.40 to 1.58 mm., averaging significantly smaller than all of the Palaearctic samples. As might be expected, they conform to the "*mixtus*" type in the allometric characters just described.

Geographic variation of queen appendage pilosity is apparently reflected in the worker caste, since the "*umbratus*" character is rare or absent in workers from the Mediterranean perimeter. When pilosity in northern series is plotted against size, a simple allometric regression zone is obtained (Fig. 16). As in the queen, there is no evidence of a breakdown into two or more species. Much the same relationship apparently holds for cephalic pilosity, one of the two characters mentioned by Stärcke. Stärcke's second worker character, petiole shape, grades through from one extreme (straight dorsal border) to the other (deeply concave border), as already stated in the diagnosis. It does not show any geographic trend.

Asiatic queens. Umbratus is evidently less common in eastern Asia than in Europe and North America, being outnumbered in collections from there by *L. rabaudi.* I have seen only seven queens in the course of this study, including the holotypes of *silvestrii* Wheeler and *osakana* Santschi, and specimens from Nishiashoromura, Hokkaido (Matsuda leg.; Yasumatsu Coll.), Tokyo (L. Gressitt leg.; MCZ), Ryūjin, Wakayama Pref., Honshu (M. Azuma leg.; MCZ), and Sian Air Field, Shensi, China (W. L. Brown leg., MCZ). These are consistently large, HW ranging between 1.68 and 1.84 mm., and have somewhat more quadrate heads than European queens of comparable size, i.e. the heads taper less strongly anterior to the eyes. The *silvestrii* holotype and Ryūjin queen have an unusual pilosity feature: the hairs on the scapes and legs are very dense and relatively short;

those on the legs are predominantly subdecumbent, while those on the scapes are subdecumbent-suberect. The *osakana* holotype and Tokyo queens are not distinguishable from large northern European *umbratus* in pilosity, and hardly distinguishable in head shape. The Hokkaido and Shensi specimens are conveniently intermediate in pilosity between the *silvestrii* holotype and northern European *umbratus* and within range of variability of the latter in head shape. In general, the eastern Asiatic material is the most divergent of any single geographic sample, but the meager evidence available weighs against according it even conventional subspecific rank.

Lebanese queens. Two alate queens from the mountain above the Kammouha Plain (K. Christiansen leg.; MCZ) are peculiar in that the petiolar scale seen from the side is abruptly narrowed at midlength, so that the upper half is conspicuously thinner than the lower. In frontal view the dorsal margin is deeply and angularly emarginate. Both features represent extremes in what is normally a very variable structure in the European population. In other ways the queens are typical *umbratus*.

Worker eye size. The North American population as a unit has proportionately larger eyes, i.e. a higher EW-HW regression zone, than the European population as a unit, but there is still a great deal of overlap between the two (Fig. 17).

DISTRIBUTION. *Umbratus* is widespread over both Eurasia and North America. Our present knowledge of its distribution in Eurasia is unfortunately limited due to its past erroneous identification with the cryptic species *rabaudi* and the present dearth of diagnostic characters in the worker. I have listed below those records which I have verified myself through examination of the queen caste.

ENGLAND: "Wand" (MCZ). NORWAY: Asker, Oslo (H. Holgersen leg. and Coll.); Roa, Opland (Holgersen leg. and Coll.). SWEDEN: Ludgo, Södermanland (K.-H. Forsslund Coll.); Ekerö, near Stockholm (Forsslund leg. and Coll.); Österåker, Stockholm (Forsslund leg. and Coll.); Enköpling, Uppsala (Forsslund leg. and Coll.); Grangärde, Kapparberg (Forsslund leg. and Coll.). FINLAND: Helsinki (O. Wellenius leg.; USNM). NETHERLANDS: Den Dolder (A. Stärcke leg.; Forsslund Coll.); Roermond (J. K. A. van Boven leg.; MCZ). GERMANY: Tharandt, near Dresden (W. M. Wheeler leg.;

MCZ). SWITZERLAND: Roveredo (H. Kutter leg. and Coll.); Flawil (Kutter leg. and Coll.); Bruggen (Kutter leg. and Coll.); Saint Aubin (Kutter leg. and Coll.); Morges (A. Forel leg.; MCZ); Lausanne (M. Bibikoff leg. and Coll.). AUSTRIA: Plöeken Region (C. Mader leg.; Holgersen Coll.). CZECHOSLOVAKIA: Kroměříž (O. Fiala leg.; MCZ). HUNGARY: Nagytétény (P. Röszler leg.; MCZ). ITALY: San Nassaro, Lombardy (Kutter leg. and Coll.); Valbrona, Lombardy (B. Finzi leg.; MCZ); Monte Vederne, Venezia Tridentina (B. Finzi leg.; MCZ); Trieste (Finzi leg.; MCZ); Roiano, near Trieste (Finzi leg.; MCZ). YUGOSLAVIA: Parenzo and Momiamo, Istrian Peninsula (Finzi leg.; MCZ); "Podcetrtek" (Jaeger leg.; MCZ); eastern Bosnia (Milch leg.; MCZ). ALBANIA: Tomoriea (Ravasini and Lona leg.; MCZ). LEBANON: Mt. above Kammouha Plain, 1500 meters, 2 alate queens (K. Christiansen leg.; MCZ).

The several verified Asiatic records have been discussed in the section on geographic variation. There are a great many literature records from Eurasia available, but these are of course rendered useless in the absence of their recognition of *L. rabaudi*. Several might be mentioned, however, in order to obtain a more complete picture of the range of the "*umbratus* group" in Eurasia: Daghestan (Kuznetzov-Ugamskij, 1929b); Dairen (Eidmann, 1929); Tatsienlu, Sikang (Eidmann, 1941); Nikolsk-Ussurijsk, Soviet Maritime Territory (Kuznetzov-Ugamskij, 1929a). In addition, I have seen indeterminate workers belonging to the group from Genzan, Korea (S. Kumashiro leg.; Yasumatsu Coll.) and Harbin, Manchuria (Y. Mori leg.; Yasumatsu Coll.).

In eastern North America *umbratus* occurs from Nova Scotia south to the Gulf States. I have verified the following records from southeastern Canada. NOVA SCOTIA: Bridgewater, a dealate queen (MCZ). NEW BRUNSWICK: Shediac Cape (Hubbard leg.; MCZ). QUEBEC: Kingsmere (MCZ); Hull (W. M. Wheeler leg.; MCZ). ONTARIO: Toronto (MCZ); Ottawa (MCZ); Plantagenet (E. O. Wilson leg.; MCZ); Point Pelee and Pelee Island (M. Talbot leg. and Coll.). *Umbratus* is generally abundant from New England south to the southern Appalachians of North Carolina and Tennessee. It is rare in the Gulf States, being known only from the following several records. GEORGIA: Blood Mountain, Union Co. (H. T. Van-

derford leg.; USNM). FLORIDA: "Camp Torreya", Liberty Co. (H. K. Wallace leg.; UMMZ, MCZ). ALABAMA: Decatur, Morgan Co. (Wilson leg.; MCZ); Fayette, Fayette Co. (B. D. Valentine leg.; MCZ); Tuscaloosa (Wilson leg.; MCZ); Pollard, Escambia Co. (Wilson leg.; MCZ). MISSISSIPPI: Boyle, Bolivar Co. (M. R. Smith leg.; MCZ).

Westward, *umbratus* is abundant through North Dakota, as evidenced by the large numbers of collections made in many localities in that state by G. C. Wheeler and his students. It appears to be relatively common in the southern Rockies, but sparse to absent over most of the rest of western North America. There is a good possibility that its distribution west of the Great Plains is influenced in large part by competition from related species. It has never been taken within the range of *L. vestitus*, i.e. from northern California to British Columbia and northern Idaho. Moreover, in the mountainous areas where its range overlaps that of *L. subumbratus*, it tends to occur at lower elevations than that species and, so far as I know, the two have never been taken in the same immediate locality.

Following are the records from west of North Dakota accumulated during the present study. MONTANA: "Beaver Creek", 6300 feet (S. J. Hunter leg.; MCZ). IDAHO: Twin Falls (A. C. Cole leg. and Coll.). COLORADO: "Beaver Ranch" (W. M. Wheeler leg.; MCZ). UTAH: Kigalie Ranger Station, La Sal National Forest (C. T. Brues leg.; MCZ). ARIZONA: Williams, 7000 feet (Wheeler leg.; MCZ). NEW MEXICO: Ute Park, Colfax Co., 7400 and 7450 feet (2 series, A. C. Cole leg. and Coll., MCZ); Cimarron Canyon, 15 miles north of Cimarron, Colfax Co., 7100 and 7450 feet (2 series, Cole leg. and Coll.); Raton, Colfax Co. (C. T. Brues leg.; MCZ); Sapello Canyon, Beulah area, San Miguel Co., 7000 feet (Cole leg. and Coll., MCZ); Sandia Mountains, Bernalillo Co., 7700 feet (Cole leg. and Coll., MCZ); Mogollon Mountains, Catron Co., 8600 feet (Cole leg. and Coll., MCZ).

ECOLOGY. In the face of the revelation that *umbratus* has a common and hitherto poorly known Palaearctic sibling, *rabaudi* (Bondroit) (=*meridionalis* Bondroit), the great mass of European literature pertaining to this species and its many synonyms cannot be accepted without major qualifications. It is in fact very probable that much of the literature deals with *rabaudi*

instead of *umbratus*. Among the European authors, only Stärcke (1937) seems to have fully realized the status and common occurrence of *rabaudi* and taken this taxonomic information into account in his ecological work. We are still very much in the dark as to whether the two species differ ecologically to any appreciable extent. In the following brief resumé, reference to European literature on *umbratus* is made with the understanding that both species may be included.

In Europe, according to Gösswald (1932), Zimmermann (1934), Donisthorpe (1927), and others, *umbratus* is less common than the prominent members of *Lasius s. s.* It prefers dry areas and rarely nests in moist soil; Skwarra (1929) found it very rare on the wet Zehlau moors of East Prussia. It usually nests under rocks, but also occurs in rotting wood (including the timbers of houses), at the foot of trees, or in open ground. On occasion it builds mounds. Its preferred habitat is woodland, but it has also been taken along forest borders and in cultivated fields. In North America, where no sibling comparable to *rabaudi* is yet known, *umbratus* differs from the European population in that it prefers moist soil, but it still shows the same latitude in specific nesting sites. The majority of colonies have been taken under stones, while the rest have been taken in or about rotting logs and stumps. I do not know of any case of this ant building mounds or even nesting in the open soil in North America, as it (or *rabaudi*) has been known to do in Europe. In the northern U. S. east of the Mississippi River, *umbratus* is limited mostly to moist woodland, where it occurs under a wide variety of conditions of soil texture and insolation. In Alabama and Florida, at the southern extremity of the range, all of the several colonies recorded were found in rotting logs and stumps in swampland. In the western U.S., all of the collections with ecological data that I have examined were made under rocks in open forest and along or near forest borders. In New Mexico, A. C. Cole took this species between 7100 and 8000 feet, always under rocks but under variable conditions of soil moisture and vegetation, e.g. dry soil with scattered juniper and pine or oak and pine, moist soil in a clearing near a hardwood forest, and moist soil in an open grassy area.

As is the case in other species of *Lasius,* observations on the food habits of *umbratus* are entirely fragmentary and anecdotal.

Umbratus is generally thought to be subterranean and to subsist primarily on the excreta of aphids and coccids, since these insects are often found in great numbers in the galleries with the ants (cf. Donisthorpe, 1927, and Gregg, 1944). However, in Holland, Stärcke (1937) has observed workers foraging aboveground at night and carrying insects to the nests presumably for use as food. Brown (pers. commun.) has also observed workers aboveground on cloudy days in Pennsylvania.

A number of nuptial flights recorded by Donisthorpe (1927), Crawley (1915), and Eidmann (1926) suggest a long flight season in Europe, extending from as early as August 8 (Crawley) to as late as October 7 (Eidmann). However, there is again no way of knowing whether these records might not represent the overlapping periods of the two species *umbratus* and *rabaudi*. Winged queens, determined by me as authentic *umbratus*, have been taken in Europe on the following dates: IV-4, V-11, VI-9, VI-12, VII-24, VII-31, VIII, VIII, VIII-(15-20), VIII-22, VIII-28, IX-3, IX-10, IX-13, IX-16, IX-17, IX-29; these do not involve any apparent geographic trend and by themselves may indicate an unusually long flight period.

The situation in North America is somewhat similar. I have observed queens in flight in the environs of Boston, Mass., in September during two recent seasons. Lone dealate queens were found wandering above ground at Cambridge, Mass., on September 5, 1952, and October 2, 1953, and at Plantagenet, Ontario, on June 30, 1952. Dates on which winged forms have been taken alone or *in nido* cover the same period, as shown by the following random sample: VI-28, VII-8, VII-27, VIII-1, VIII-8, VIII-13, VIII-13, VIII-18, VIII-20, VIII-31, IX-1, IX-5, IX-9, IX-27, X-14, X-28, X-29. Since there are no known sibling species to complicate the picture in North America, the data here suggest that on this continent at least umbratus has an unusually long nuptial season.

There is no evidence to indicate that the reproductives of *umbratus* build aerial swarms during their nuptial flights, as do those of *niger* and *flavus*, although this does not preclude the possibility. Eidmann (1926) observed queens of *umbratus* (or *rabaudi?*) flying singly in Germany, and I have observed definitely determined *umbratus* queens flying singly on two occasions in the Boston area.

Donisthorpe (1927), Crawley (in Donisthorpe, *ibid.*), Gösswald (1938), and Hölldobler (1953) have reported in detail on the colony founding behavior of "*umbratus*" and "*mixtus*". The normal hosts are *L. niger* and *L. alienus*. Under both field and laboratory conditions dealate *umbratus* queens attack host workers as they encounter them away from the nests, seizing them up the mandibles and carrying them about as they resume foraging. Their victims are usually killed by this treatment and may eventually be eaten. With the fulfillment of this *Mordinstinkt,* as Hölldobler calls it, and the presumed acquisition of the host odor, the queens are ready and able to enter host colonies, although they may be subjected to further attack before acquiring final acceptance. Unfortunately, the authors who have witnessed this phenomenon failed to make a convincing distinction between *umbratus* and *rabaudi*, and specimens were not saved to allow corroborative determinations during the present revision.

During the falls of 1952 and 1953 I collected numerous dealate *umbratus* queens at Cambridge, Mass., and tried introducing them into colonies and colony fragments of *sitkaensis, alienus,* and *neoniger,* but never obtained a complete adoption and saw no evidence of the *Mordinstinkt* behavior. I have also worked on the theory that the *umbratus* may join recently fecundated host queens, since both host and parasite queens are often found in species-pure groups under rocks following nuptial flights. Various attempts to bring *umbratus* and *neoniger* queens together, including placing them in the same chamber while chilled, have so far failed; the reason may be, however, that *neoniger* is not a natural host. I would like to suggest, on what admittedly constitutes negative evidence, that behavior in the population I studied may differ from that in the European populations. If true, this could be due either to geographic variation or to the fact that the European authors were using *rabaudi* instead of *umbratus*. Only additional research accompanied by careful determinations will settle the matter.

Niger and *alienus* probably serve as hosts of *umbratus* in North America as they do in Europe. I have seen two mixed *niger-umbratus* nest series from Ute Park, New Mexico (A. C. Cole leg. and Coll., MCZ) and one *alienus-umbratus* series from Beatty, Pennsylvania (Schmitt leg.; MCZ). The Beatty *um-*

bratus are minimas. Buren (1944) found a single dealate "*aphidicola*" queen with a depauperate colony of "*flavus nearcticus*", but to my knowledge there has been no additional evidence forthcoming that this or any other *Chthonolasius* uses species of *Cautolasius* as hosts.

SYNONYMY. *Formica mixta* Nylander. Holotype, a dealate queen in the Helsinki Museum. The status of this important synonym has already been fully discussed in the section on geographic variation.

Formica aphidicola Walsh. The location of the types of this form is unknown. They may be in the Academy of Natural Sciences, Philadelphia, although I was unable to find them during a brief visit there. As I have already shown, the North American population tends to differ as a unit in queen body size and worker eye size but the overlap in these two characters is too great to allow even a conventional subspecific division.

Formica affinis Schenck. What are probably the long-forgotten syntypes of this form have been located in the section of the Schenck Collection owned by the University of Marburg. Specimens sent me by Prof. E. Kessel of the Zoologisches Institut are labelled "Lasius affinis Sck" but lack locality or type data. However, these are the only specimens in the collection determined as *affinis,* all three castes are represented as was stated to be the case with the type series, and all fit Schenck's original description. The many commentaries written in the past on the status of *affinis* (along with the series I have seen determined as this species by various European authorities) leave no doubt that *affinis* must stand or fall on the single presumed distinction that the petiolar scale is proportionately higher in *affinis* than in the typical *umbratus.* That it must fall has been determined by measuring the scale height against the head width of European series of *umbratus.* The putative *affinis* queen syntype has a scale height (measured from the bottom of the ventral lobe to the dorsal crest) of 1.08 mm. and a HW of 1.64 mm. *Umbratus* series with the same approximate HW (1.58-1.73 mm.) showed every gradation in scale height from 0.83 mm. to 1.10 mm. It is obvious that "*affinis*" represents only one extreme in this highly variable *umbratus* character. The queen syntype is also notable in having a deeply emarginate scale, but as previously noted this

is also within the normal *umbratus* range of variation. (See Pl. 2, Fig. 1.)

Lasius umbratus var. *mixto-umbratus* Forel and *L. umbratus* var. *affino-umbratus* Donisthorpe. These two varieties were erected to cover intermediates between the two major variants *mixtus* and *affinis* and therefore automatically fall into the synonymy.

Lasius umbratus var. *exacutus* Ruzsky. This variety was based on workers with high, tapering, emarginate petiolar scales and hairy scapes and tibiae. The lack of types notwithstanding, it is probably safe to conclude from the description alone that *exacutus* falls within the normal range of variation of *umbratus*. At the same time, of course, there is no way of determining whether this and other forms under *umbratus* which have been based on the worker caste alone are really *umbratus* and not *rabaudi*, since no characters have been found to separate the workers of these two sibling species.

Lasius umbratus var. *przewalskii* Ruzsky. Like *exacutus* this variety is characterized by a high, tapering petiolar scale. It differs from *exacutus* in that the dorsal crest is less deeply emarginate, and the scapes and tibiae lack standing hairs. Like *exacutus*, it is probably well within the normal range of variation of the *umbratus* group. It is not clear how Ruzsky thought he could distinguish *exacutus* and *przewalskii* from *affinis*, since they share the same principal diagnostic character, but this is of little consequence so long as the names remain in synonymy.

Formicina umbrata distinguenda Emery. This is the name applied to larger southern European queens lacking standing tibial hairs and will have priority if some future taxonomist feels the need to apply a trinomen to the southern population.

Formicina belgarum Bondroit. Reduced to a variety by Stärcke, this form is based on trivial characters in pilosity, petiole outline, color, etc., and seems to be well within the range of normal variation of the European population.

Lasius bicornis var. *citrina* Emery. Lectotype by present selection, a worker in the Emery Collection labelled "Monte Gargano 1907". This specimen is a typical *umbratus* (or *rabaudi*), with the petiolar emargination forming an angle of about 100°, easily within the range of variation of *umbratus*. The naming of this form undoubtedly resulted from Emery's erroneous conception

of the species line separating *umbratus* and *bicornis*.

Lasius umbratus var. *viehmeyeri* Emery. The head shape of the queen figured by Emery is not far divergent from what would be expected in very large specimens conforming to normal allometric variation. The shining sculpture mentioned by Emery is inconsistent with the known allometric trend in *umbratus,* but otherwise *viehmeyeri* does not seem to differ significantly from this species.

Lasius silvestrii Wheeler. The status of this form has been discussed in the section on geographic variation.

Lasius viehmeyeri var. *dalmatica* Stärcke. New and convincing evidence for the specific status of *viehmeyeri* must be produced before *dalmatica* can be considered as anything more than a trivial variant of *umbratus.*

Lasius umbratus var. *hirtiscapus* Stärcke. This is undoubtedly the extreme hirsute form of the northern population previously discussed in the section on geographic variation.

Lasius umbratus distinguendus var. *cereomicans* Stärcke. This is a trivial variety established on what appears from the description to be a fortuitous, non-genetic character.

Lasius silvestri [!] var. *osakana* Santschi. The status of this form has already been discussed in the section on geographic variation. The holotype is nearly identical with typical northern European queens of *umbratus.*

Chtonolasius [!] *affinis* var. *nyárádi* Röszler. On morphological evidence alone, this variety must fall into the synonymy along with *affinis.*

Lasius umbratus epinotalis Buren. I have been able to examine a single paratype of this form in the Creighton Collection. Contrary to the statement of Creighton (1950), eye size in this specimen does not link it to *subumbratus*, but rather places it in the center of the EW-HW regression zone of the North American population of *umbratus* as plotted in Figure 17. Furthermore, differences in size, antennal conformation, propodeum shape, and pilosity as given by Buren and Creighton have proven upon critical examination to be trivial or non-existent. At the most, *epinotalis* has unusually sparse gastric pubescence for an *umbratus,* but it is still within the extreme range of variation shown by that species. Examination of additional material from Iowa (King Coll.) has shown that *epinotalis* is not a representative of any significant geographic trend in this character.

Lasius rabaudi (Bondroit)

(Subg. *Chthonolasius*)

Formicina rabaudi Bondroit, 1917, Bull. Soc. Ent. Fr., **86:** 177; queen; original description. Type locality: Amélie-les-Bains, Pyrénées-Orientales, France.

Formicina meridionalis Bondroit, 1919, Ann. Soc. Ent. Belg., **88:** 143; original description. Type locality: Aveyron, France. NEW SYNONYMY.

Lasius tibialis Santschi, 1926, Bull. Soc. Sci Nat. Maroc, **16:** 208; queen; original description. Type locality: Grand Atlas Mountains, Morocco. NEW SYNONYMY.

DIAGNOSIS. A common Palaearctic species very close to *umbratus* and safely distinguishable only in the queen caste.

Queen. (1) Scapes and tibiae conspicuously flattened, so that the minimum width of the scape at the midpoint is 0.10 mm. or less (Fig. 15).

(2) Funicular segments tending to be proportionately longer than in *umbratus.* In the *rabaudi* series examined, funicular segment III varied 1.47-1.87 × longer than broad, while an equivalent sample of Eurasian *umbratus* varied 1.00-1.50 × longer than broad, with only one specimen exceeding the *rabaudi* minimum of 1.47 ×.

(3) The shape of the petiole characteristic, and less variable than in *umbratus:* in frontal view subquadrate, nearly as broad at the dorsal crest as at the level just above the frontal foramen, and with a rounded to angulate dorsal emargination. European series have concave to straight lateral margins; Japanese series may have convex margins in addition.

Worker. (1) The most reliable queen character, the flattening of the scape, seems to be reflected in the worker, but there is considerable overlap between the two species, and probably a majority of worker series unaccompanied by queens cannot be certainly placed. Series of *umbratus* accompanied by queens are characterized as follows: in workers with maximum midpoint scape width of 0.10-0.12 mm., the minimum midpoint width was always 0.08 mm. or more. In the two series of *rabaudi* accompanied by queens ("Morogi-Mura" and Roermond) the minimum width was distinctly less than 0.08 mm. However, other series unaccompanied by queens, and therefore not determinable by reference to the *rabaudi* type, completely overlapped determined

umbratus and extended far below the identified *rabaudi* series, to minimum width 0.06 mm.

(2) The "Morogi-Mura" and Roermond series and others with greatly flattened scapes also had abundant standing hairs on the scapes, which character is frequent in *umbratus* only in northern Eurasian samples.

Male. Males associated with very flat-scaped workers from Roermond are rather small compared to *umbratus* (HW about 0.98 mm.) and show certain expected allometric differences in mandibular and petiolar structure, but in this and every other character they are within the extreme range of variation of *umbratus.* There is no appreciable flattening of the scapes.

HOLOTYPE. An alate queen in the Bondroit Collection. HW 1.73 mm., SL 1.53 mm., SI 89; maximum width of scape at midlength 0.15 mm., minimum width 0.08 mm.; length of third funicular segment 0.17 mm., width 0.11 mm. The relative length of the antennae and the length of the cephalic hairs slightly exceed those of any other European series examined but are within the range of variation of the Japanese series and nearly identical with the *tibialis* holotype from North Africa. The petiolar scale is typical of the species; the sides are straight in frontal view. There can be little doubt that, despite its somewhat atypical nature, this specimen belongs to the same species later called *meridionalis* by Bondroit and Stärcke. Bondroit's opinion concerning the holotype's resemblance to *Dendrolasius* is manifestly erroneous.

GEOGRAPHIC VARIATION. Nearly all European queens examined have the same frontal petiolar outline, shallow emarginate dorsal border and feebly concave sides. The types of *rabaudi*, from southern France, and *tibialis,* from North Africa, have petioles with straight sides and slightly deeper dorsal emarginations. A queen from Ashoromura, Hokkaido, and one from Hikosan, Kyushu, have concave sides, while other Japanese series have straight to feebly convex sides. The Japanese series also show variation in the dorsal emargination from shallow-rounded to moderate-angulate. The Japanese series and *rabaudi* and *tibialis* holotypes have proportionately longer antennae.

The Japanese series have denser body hair than the European and as a rule hairer scapes, although the Roermond series exceeds one Hikosan queen in this respect. In both the queen and

worker the standing hairs on the head and gaster tend to be proportionately longer in the Japanese series than in the European.

DISTRIBUTION. Queens determined as *rabaudi* and included in the plot in Figure 15 came from the following localities. ENGLAND: "Inghilterra Crawlei" (from Finzi Coll. in MCZ). SWEDEN (all Bo Tjeder leg., Forsslund Coll.); Kåseberga, Kristianstad, VII-22-1950; Löderup, Kristianstad, VII-21-1950; Högsrum, Öland. HOLLAND: Den Dolder, three series, VII-15-1943, VII-24-1944, VII-25-1944 (A. Stärcke leg.; Holgersen Coll.); Roermond, VII-27-1947 (J. K. A. van Boven leg.; USNM). FRANCE: Aveyron (*meridionalis* holotype); Amélie-les-Bains, eastern Pyrenees (*rabaudi* holotype). SWITZERLAND: Zermatt, VIII-12-1919 (H. Kutter leg. and Coll.). AUSTRIA: Vienna (MCZ). ITALY: Lavarone, Venezia Tridentina (MCZ); Trieste (MCZ); Barcola, near Trieste (MCZ). YUGOSLAVIA: Dubrovnik (Novak leg.; MCZ). MOROCCO: Grand Atlas Mountains (*tibialis* holotype). HOKKAIDO: Ashoromura, VIII-9-1949 (R. Matsuda leg.; Yasumatsu Coll.). HONSHU: Tokyo, VI-6-1931 and VI-20-1931 (L. Gressitt leg.; MCZ). KYUSHU: Hikosan, 2 series VII-6-1939, VIII-5-1940 (Yasumatsu leg. and Coll.); Sobosan, VII-16-1931 (Esaki and Fujino leg.; Yasumatsu Coll.). SHIKOKU: "Morogi-Mura", VI-25-1952 (Okamoto leg. and Coll., MCZ); Yoshino (Okamoto leg. and Coll.). Workers unaccompanied by queens, but with greatly flattened scapes, have been recorded from Roermond (with males, VII-17-1947; van Boven leg.; MCZ); Hikosan, Kyushu (Yasumatsu leg. and Coll.); Hirooka and Mt. Kajigamori, Shikoku (Okamoto leg. and Coll., MCZ).

ECOLOGY. Stärcke (1937) has obtained the experimental adoption of *rabaudi* (=*meridionalis*) queens by *L. niger* workers. Later observations by the same author suggest that *rabaudi* can serve in turn as the host for *L. fuliginosus* (see the section on ecology of that species).

SYNONYMY. *Formicina meridionalis* Bondroit. Holotype, a dealate queen in the Bondroit collection. HW 1.63 mm., SL 1.38 mm., SI 84; maximum width of scape at midpoint 0.16 mm., minimum width 0.09 mm.; length of third funicular segment 0.15 mm., width 0.10 mm. This specimen is somewhat more typical of the European population in relative antennal length and

cephalic pilosity than is the *rabaudi* holotype.

Lasius tibialis Santschi. Holotype, a queen in the Santschi Collection. HW 1.73 mm., SL 1.54 mm., SI 89; maximum width of scape at midpoint 0.17 mm., minimum width 0.10 mm.; length of third funicular segment 0.18 mm., width 0.10 mm. This specimen is nearly identical in every respect with the *rabaudi* holotype.

Lasius speculiventris Emery

(Subg. *Chthonolasius*)

Lasius speculiventris **Emery, 1893, Zool. Jahrb. Syst., 7: 641–642; worker, male; original description. Type locality: Caldwell, New Jersey.**
Lasius umbratus speculiventris**, Wheeler, 1910, Psyche, 17: 242.**

DIAGNOSIS. An eastern North American species closely related to *umbratus,* but differing by its very sparse gastric pubescence and tendency toward denser cephalic and appendage pilosity.

Worker. (1) Central area of exposed second gastric tergite, exclusive of the posterior strip, almost completely devoid of pubescence of any kind and with only a few widely scattered erect hairs, its cuticular surface extremely smooth and shining. The third and posterior tergites are usually very similar in this respect to the second, but the first tergite may have the bare area limited to a median longitudinal strip as narrow as one-fourth the width of the gaster (E. S. George Reserve, Mich.). Series at the opposite extreme (Caldwell, N. J.; Volo, Ill.; Chicago, Ill.) have no pubescence whatsoever on the gastric tergites except for thin zones along the posterior tergital margins.

(2) Standing appendage and cephalic pilosity ranging from extremely dense (scapes and legs covered with abundant, predominantly subdecumbent to erect hairs, and the margin of the head seen in full face from the mandibular insertions to the anterior borders of the eyes with more than 20 erect hairs) to less dense than the extreme hirsute form of *umbratus* (hairs on the scapes and legs mostly appressed-decumbent and seldom standing, and only one or two erect hairs along the genal contour). The type series exhibits the first extreme, and the Urbana, Ill., series, the second. There is no evident correlation between

the density of the cephalic and anterior appendage pilosity and the density of the gastric pubescence.

Queen. (1) Gastric pubescence as in worker. Dorsal surfaces of second, third, and fourth tergites exclusive of the posterior strips almost completely devoid of pubescence. Dorsal surface of first tergite covered with appressed pubescence except for a thin, longitudinal, median strip about 0.15 mm. in width.

(2) Scapes and legs hairier than in all North American *umbratus* seen but still within range of variation of Eurasian series, Scape densely covered with short, predominantly decumbent hairs. Femora and tibiae with dense appressed pilosity and scattered short but outstanding decumbent hairs.

(3) In all other aspects apparently identical to *umbratus.* Extreme HW range 1.53-1.62 mm.

Male. (1) At least the median longitudinal fourth of the second and posterior gastric tergites devoid of pubescence, its cuticular surface smooth and shining; in the type series the entire dorsal gastric surface is devoid of hairs and strongly shining.

(2) Standing hairs more abundant on the head and alitrunk than in North American *umbratus.* In the type series, but not in another series from Ramsey Co., Minn., erect hairs are abundant along the genal contour viewed in full face.

(3) Extreme HW range 1.00-1.21 mm.

LECTOTYPE. By present selection, a worker in the Museum of Comparative Zoology labelled "Caldwell, N. J., Sept. 11 '88." Synnidotypes are in the Museum of Comparative Zoology, Emery Collection, American Museum of Natural History, and United States National Museum. The extreme nature of this series with respect to the rest of the species population has already been mentioned.

DISTRIBUTION. This species is widespread in the eastern United States and seems to be most common in the Great Lakes district. Following are all of the records accumulated during the present study. NEW JERSEY: Caldwell, Essex Co. (type series). PENNSYLVANIA: Lemont, Centre Co. (W. L. Brown leg.; Pennsylvania State University Coll.). ILLINOIS: Chicago (M. Talbot leg. and Coll., MCZ); New Lenox, Will Co. (Talbot leg. and Coll.); Volo, Lake Co. (Talbot leg. and Coll.). MICHIGAN: E. S. George Reserve, Livingston Co., winged queens collected as pupae VIII-1-1953 and preserved after eclo-

sion VIII-10-1953 (Talbot leg. and Coll.); Ann Arbor (J. Dawson leg.; MCZ); East Lansing, winged queens IX-1899 (USNM); Litchfield, Hillsdale Co. (A. M. Holmquist leg.; USNM). MINNESOTA: Ramsey Co., winged queens and males VIII-25-1922 (A. T. Hertig leg.; USNM). IOWA: Iowa City (USNM). KANSAS: Douglas Co., winged queen, June (E. S. Tucker leg.; U. of Kans. Coll.). Series recorded by Cole (1940) from the Great Smoky Mountains of Tennessee as *speculiventris* have been re-examined and determined as *umbratus.*

ECOLOGY. Dr. Talbot has kindly supplied me with ecological notes on several of her collections. This species nests under a variety of conditions. At Volo it was taken in natural hummock in marshy ground near a larch-sphagnum bog. At New Lenox two colonies were found in a pasture, deep in the sod under rocks set in a dry ditch bank. At the E. S. George Reserve a huge colony was found beneath a layer of red woody soil under a dead standing tree in oak-hickory woods; the ants had galleried the roots of the dead trees into thin partitions.

Lasius vestitus Wheeler
(Subg. *Chthonolasius*)

Lasius umbratus vestitus Wheeler, 1910, Psyche, **17**: 242; queen; original description. Type locality: Moscow, Idaho.

Lasius vestitus, Creighton, 1950, Bull. Mus. Comp. Zool., **104**: 425.

Lasius pilosus M. R. Smith, 1934, Ann. Ent. Soc. Amer., **27**: 384; worker; original description. Type locality: Moscow, Idaho (probably Moscow Mountain, near Deary, Latah Co.). NEW SYNONYMY.

DIAGNOSIS. A western North American species closely related to *umbratus* but easily distinguished in both the queen and worker castes by its unusual body pilosity.

Queen. (1) Entire body, including the gula, genae, and outer lateral margins of the mandibles, densely covered with long, predominantly erect, silky-yellow hairs. Those on the gaster exceptionally uniform in length and inclination, lending the gaster a brush-like appearance in side view; the longest hairs on the tergites are 0.25 mm., approximately the maximum width of the hind tibia midpoint. These tend to be sparser and shorter on the sides of the alitrunk than on the dorsum, not exceeding 0.14 mm. The numerous hairs set along the dorsal petiolar crest

tend to be curved and many are even flexous. The scapes, femora, and tibiae with abundant shorter, predominantly subdecumbent-erect hairs on all surfaces. Entire body covered with dense, appressed pubescence.

(2) Total size averaging smaller than other *umbratus*-complex members, and appendages averaging proportionately longer. HW and SI of all available specimens are as follows: 1.37 mm., 89; 1.42 mm., 90; 1.42 mm., 86; 1.42 mm., 87; 1.43 mm., 89; 1.43 mm., 90; 1.44 mm., 88; 1.46 mm., 85; 1.46 mm., 89; 1.52 mm., SI not measurable.

(3) Body color uniformly medium brown, the appendages light brown.

Worker. (1) Exposed gastric tergites evenly covered with abundant, long, suberect-erect hairs; the longest over 0.12 mm., or exceeding four-fifths the maximum width of the hind tibia at its midlength. At least a few scattered standing hairs present on the scapes, femora, and tibiae.

(2) Size apparently about the same as in *umbratus;* PW range 0.66-0.73 mm.

The worker is generally very similar to the large, hairy Eurasian form of *umbratus*, differing slightly in the length of the body pilosity as exemplified in the above description of the gastric pilosity. At the same time it is strikingly different from the sympatric North American form of *umbratus* and can be separated at once by its possession of standing hairs on the scapes and tibiae.

HOLOTYPE. A queen in the Museum of Comparative Zoology, now in poor condition, with the head missing and much of the body pilosity broken down or worn off. Other queens in the same collection, however, show a detailed correspondence in all features that could be studied.

GEOGRAPHIC VARIATION. Workers from Moscow have a notably denser pilosity than others from Corvallis; seta count of the single measurable Moscow specimen is 13, seta counts of the measurable Corvallis workers are 2, 3, 5, and 11. This difference, however, is not manifested between the holotype, from Moscow, and queens from farther west.

DISTRIBUTION. *Vestitus* appears to be concentrated along the Pacific Coast, but extends eastward at least as far as western Idaho. CALIFORNIA: Lassen Pk. Trail, Shasta Co., winged

queen VII-14-1947 (D. W. Adams leg.; USNM); Requa, Del Norte Co. (C. D. Duncan leg.; UMMZ). OREGON: Corvallis, workers II-10-1936, a winged queen V-24-1935 (G. Ferguson leg.; MCZ); Alsea Mountain, Benton Co., winged queen V-18-1947 (H. A. Scullen leg.; USNM); Rickreall, Polk Co., a winged queen VII-15-1933 (J. Schuh leg.; MCZ); Zigzag Glacier, Mt. Hood, winged queens VII-7-1927 (P. J. Darlington leg.; MCZ). BRITISH COLUMBIA: Forbidden Plateau, Vancouver Island, a winged queen VII-13-1935 (J. D. Gregson leg.; USNM); Nanaimo (E. C. Van Dyke leg.; CAS). IDAHO: Moscow (*vestitus* holotype, *pilosus* nidotypes).

SYNONYMY. *Lasius pilosus* M. R. Smith. There can be little doubt that *pilosus* represents the worker caste of *vestitus*. Although never associated in the same nest series, both have been taken at the same two localities, Moscow and Corvallis, within a relatively small section of North America in which other *Chthonolasius* are rare or absent. In July, 1952, I spent two days at the type locality searching in vain for this species. Most of the area around Moscow is under heavy cultivation, but a large stand of forest still exists on Moscow Mountain, and this is very likely the origin of the *pilosus* types, as suggested by Smith. On Moscow Mountain I collected intensively on the southern slope from pine-larch forest around 3000 feet, up through a dense *Lasius sitkaensis* population in pine-fir forest, to the summit at 5500 feet. No species of *Lasius* other than *sitkaensis* were encountered during this time.

Lasius subumbratus Viereck
(Subg. *Chthonolasius*)

Lasius umbratus subumbratus Viereck, 1903, Trans. Amer. Ent. Soc., **29:** 73; queen; original description. Type locality: Beulah, San Miguel Co., New Mexico.

Lasius subumbratus, Creighton, 1950, Bull. Mus. Comp. Zool., **104:** 424.

DIAGNOSIS. A close relative of *umbratus* sympatric with that species over most of its range from the maritime provinces of Canada to western North America and best distinguished from it by differences in body pilosity.

Queen. (1) Pilosity on anterior three gastric tergites very long (maximum length 0.24-0.27 mm., or approximately the

maximum width of the hind tibia at midlength), silvery yellow, and predominantly decumbent-subdecumbent. Similar erect hairs form a fringe around the entire dorsal and lateral margins of the petiole; these are often curved toward their tips. Pilosity of alitrunk mostly limited to the dorsal surface, from the posterior margin of the pronotum to the dorsal face of the propodeum, averaging shorter than on the gaster and petiole, maximum length about 0.24 mm., subdecumbent to erect, often curved or sinuate. Pilosity of head mostly limited to the occipital zone, averaging shorter than on the alitrunk, maximum length about 0.18 mm., predominantly subdecumbent-suberect and often curved.

(2) Averaging larger and with proportionately longer ap-

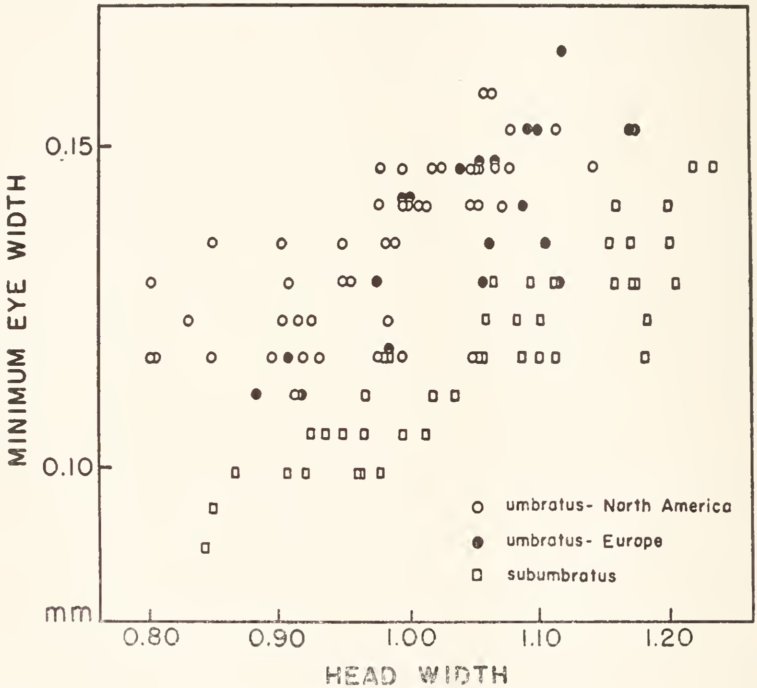


Fig. 17. Worker head width-eye width relationships in *L. subumbratus* and two geographic samples of *L. umbratus*. Further explanation in text. Nest series chosen at random; no more than two workers per series were measured.

pendages than the sympatric North American population of *umbratus*. Extreme range of HW with attendant SI of series examined 1.56 mm., 85; 1.74 mm., 83.

(3) Color averaging lighter than in *umbratus*. Body typically medium yellowish brown, head somewhat lighter; appendages light yellowish brown.

Worker. (1) Gastric pilosity longer and denser than in *umbratus*. The hairs on the first tergite with a maximum length of about 0.10 mm., or about 0.6 × the maximum width of the hind tibia at its midlength, mostly decumbent-subdecumbent (occasionally tending to suberect), and dense enough for the individual hairs to overlap one another widely. Scapes, femora, and tibiae with dense, predominantly decumbent pubescence and occasional standing hairs (*umbratus* in all populations with sparser pubescence, often appressed, and the North American population always lacking standing hairs). Gaster with very sparse pubescence, not obscuring in any way the shining cuticular surface.

(2) Eyes smaller than in North American *umbratus*, the HW-EW regression zones of the two species well separated, although no single absolute measurement will suffice to separate all the series. The Eurasian population of *umbratus* connects and overlaps the two (Fig. 17).

(3) Size averaging larger than in *umbratus*. PW range 0.55-0.85 mm.

(4) Body and appendages uniformly medium yellow, lighter than most North American *umbratus* and *minutus*.

Male. (1) Gastric pilosity similar to that of worker in form and inclination, but sparser, more often subdecumbent, and showing only limited overlap between individual hairs; maximum length of hairs about 0.13 mm., or 0.9-1.1 × the maximum width of the hind tibia at midlength. Maximum length of the hairs of the posterior two-thirds of the clypeus 0.12 mm., or slightly less than 0.10 × the HW.

(2) Averaging larger than in *umbratus;* maximum range in all series studied 1.05-1.17 mm.

(3) Genitalia similar in all respects to those of *umbratus*.

HOLOTYPE. A winged queen in the Academy of Natural Sciences, Philadelphia, in good condition and showing all of the characters used in the diagnosis above. A paratopotype queen,

recently compared with the holotype, is in the Museum of Comparative Zoology.

DISTRIBUTION. Several hundred workers, queens, and males have been examined from the following localities. NOVA SCOTIA: Digby (J. Russell leg.; MCZ); Hunter Creek, Baddeck, winged queen VII-22-1936 (T. N. Freeman leg.; USNM); Bedford (W. Reig leg.; MCZ). MAINE: Bailey Island, near Brunswick (spruce woods) (K. Christiansen leg.; MCZ). MINNESOTA: "Itasca Park", winged queens VIII-14-1933 (L. W. Orr leg.; USNM). NORTH DAKOTA: Silvista, Walsh Co. (W. E. LaBerge leg.; G. C. Wheeler Coll., USNM); Devils Lake (C. Thompson leg.; UMMZ); Grand Forks (L. Monda leg.; G. C. Wheeler Coll.); SASKATCHEWAN: Regina (H. B. Leech leg.; Cole Coll., MCZ, USNM). IDAHO: Bloomington Lake, Franklin Co. (B. Malkin leg. and Coll., MCZ). MONTANA: Fish Creek Ranger Station, Glacier National Park (W. S. Creighton leg. and Coll.); Glacier National Park (R. A. Cooley leg.; MCZ); Belt, Cascade Co., dealate queen VIII-29-1933 (Creighton leg. and Coll.). WYOMING: Firehole River, Yellowstone Park, 7600 feet, winged queen VII-21-1928 (J. McDunnough leg.; USNM); Jenny Lake, Grand Teton National Park (V. M. Tanner leg.; USNM); Devils Tower National Monument (Malkin leg. and Coll., MCZ). COLORADO: Steamboat Springs, Routt Co., winged queen VII-1-1943 (CAS); Longs Peak Inn, 9000 feet, winged queen VII-15-1926 (E. C. Van Dyke leg.; CAS). WASHINGTON: Deer Park, Spokane Co., winged queens VIII-1-1938. NEVADA: Lehman Caves, Mt. Wheeler (Creighton leg. and Coll.). UTAH: Timpanogos Peak, Utah Co. (O. H. Swezey leg.; CAS); Shingle Creek, Uinta Mts. (Creighton leg. and Coll.); Mirror Lake, Uinta Mts., 11,000 feet, winged queen VIII-5-1933 (Creighton leg. and Coll.); Lake Blanche, 10,000 feet (A. W. Grundmann leg.; Cole Coll., MCZ); Monticello, Blue Mts. (Creighton leg. and Coll.); Bryce Canyon (Creighton leg. and Coll.); Long Valley Junction, Kane Co., winged queens and males VII-24-1952 (E. O. Wilson leg.; MCZ); Warner Ranger Station, La Sal Mts. (Creighton leg. and Coll.). ARIZONA: San Francisco Peaks, near Flagstaff (Wilson leg.; MCZ); Bear Wallow to Mt. Lemmon, and Mt. Lemmon, Santa Catalina Mts. (W. M. Wheeler leg.; MCZ); Shannon Forest Camp, Graham Mt. (Malkin leg. and Coll., MCZ); Rustler Park, Chiricahua

Mts. (Malkin leg. and Coll., MCZ); Ramsey Canyon, Huachuca Mts. (Creighton leg. and Coll.). NEW MEXICO: 18 miles east of Taos, 8000 feet (A. C. Cole leg. and Coll., MCZ); 5 miles east of Eagle Nest, Colfax Co., 8600 feet (Cole leg. and Coll., MCZ); Little Tesuque Canyon, near Santa Fe, 9000 feet (Cole leg. and Coll., MCZ); Tesuque Canyon, 10,000 feet, winged queens and males with workers (Cole leg. and Coll., MCZ); 14 miles south of Mescalero, Lincoln National Forest, 7925 feet (Cole leg. and Coll., MCZ).

ECOLOGY. Cole's New Mexican collections (see above) were made under stones in a variety of habitats, including a dry, open slope, an alpine meadow, and spruce-aspen, spruce-pine, and pine-aspen forests. Wheeler (1917b) found it common at Cloudcroft, New Mexico, under stones in pine forest. I found two colonies in pine-fir forest on a southern slope of the San Francisco Mountains of Arizona, one under a stone and one under a rotting log. In the southern Rocky Mountains *subumbratus* is clearly a high-elevation species; thus far it has been found only well above the lower elevational limits of sympatric populations of *sitkaensis*, *neoniger*, *crypticus*, and *sitiens*, and it ranges at least to the upper elevational limits of these species. In New Mexico Cole encountered it between 7400 and 10,000 feet, and at Cloudcroft Wheeler was unable to find it below 9000 feet. My Arizona colonies were found at about 8000 feet.

Wheeler's studies at Cloudcroft (1917b) leave no doubt that *subumbratus* is a temporary social parasite of *L. sitkaensis*. The alternate host, "*L. neoniger*," which he found nesting in open, dry situations, may be *sitkaensis* also. I have found nothing but *sitkaensis* in his collections from this locality, and this species was the only member of the subgenus encountered during my own brief visit there. According to Wheeler, *subumbratus* is abundant enough at Cloudcroft to flood the *sitkaensis* nests with queens at the time of the nuptial flight. At one spot after a nuptial flight (occurring July 6 or 7) he found dealate *subumbratus* queens in nearly every nest of the host species uncovered. He observed that these queens approach the *sitkaensis* workers in a conciliatory manner, that they are often rebuffed at first, and that they sometimes hide in the vicinity of brood piles prior to adoption. He saw one queen in the act of stealing a host pupa and another carrying an uninjured host worker.

The latter incident is reminiscent of the conditioning behavior of *umbratus* more recently described by several European authors (*q.v.*). Several *sitkaensis* colonies with recently adopted parasite queens were found, as well as two colonies containing workers of both species. From these observations Wheeler drew the conclusion that the *subumbratus* queens are by nature conciliatory, but still find it necessary to acquire some amount of the host nest odor in order to secure final adoption.

Additional evidence is available to indicate that *sitkaensis* is the principal, if not the only, host. Cole has found mixed *subumbratus-sitkaensis* colonies at Tesuque Canyon and Eagle Nest, New Mexico; the parasite workers from the latter locality are minimas and much smaller than the associated host workers. In another nest at the second locality a single dealate *subumbratus* queen was found with *sitkaensis* workers. Finally, there is in the Museum of Comparative Zoology a series of 6 dealate *subumbratus* queens associated with *sitkaensis* (Bedford, Nova Scotia; W. Reig leg.; MCZ).

Lasius minutus Emery
(Subg. *Chthonolasius*)

Lasius umbratus minutus Emery, 1893, Zool. Jahrb. Syst., **7**: 641; worker; queen, male; original description. Type locality: New Jersey, by designation of Creighton (1950).

Lasius bicornis minutus, Creighton, 1950, Bull. Mus. Comp. Zool., **104**: 421.

DIAGNOSIS. A distinctive North American species most easily recognized by the small size and unusual pilosity of the queen. (See under diagnosis of *L. bicornis* for a more detailed comparison with that species.)

Queen. (1) Smaller than *umbratus* and *bicornis*. HW of all available series ranging 1.02-1.17 mm.

(2) Entire body covered with long, coarse hairs, the longest on the first two gastric tergites longer than the greatest width of the hind tibia at its midlength. Scapes completely bare of standing hairs; tibiae bare except for a few decumbent hairs along the flexor margins of the hind tibiae.

(3) Petiole in frontal view shallowly and angularly emarginate, with very broadly rounded dorsolateral corners.

(4) The scape rounded in cross-section.

Worker. Similar to *umbratus* in habitus, but smaller and with distinctive pilosity and petiole shape.

(1) Apparently averaging and ranging smaller than *umbratus;* extreme PW range 0.52-0.69 mm.

(2) Entire body covered with long, coarse standing hairs, the longest on the alitrunk and gastric tergites at least 0.6 $\times$ as long as the maximum width of the hind tibia midpoint and usually much longer. At the same time, the scapes and tibiae completely bare except for a few decumbent hairs along the flexor margins of the tibiae. Pubescence abundant and strongly appressed.

(3) The petiole, measured in frontal view from the level of the dorsal border of the posterior foramen to the level of the dorsolateral corners, longer than its maximum width in frontal view, and usually with a distinctive shape: tapering from the broadest level (just above the foramina) to the dorsal crest and often expanding again just at the level of the crest; the dorsal margin distinctly but shallowly emarginate (Pl. 2, Fig. 4).

(4) The scape rounded in cross-section.

Male. (1) Smaller than *umbratus* and other *umbratus* complex members. HW range of limited sample measured 0.80-0.92 mm.

(2) Long, coarse standing hairs abundant over body surface, the longest on the clypeus exceeding 0.15 mm., or greater than one-sixth the head width; the longest on the first gastric tergite 0.15 mm., or 1.6 $\times$ the maximum width of the hind tibia at its midlength.

SYNTYPES. Three nidotopotype workers in the Museum of Comparative Zoology ("N. J./Aug. 25 '85/Pergande") correspond well to syntype workers borrowed from the Emery Collection ("Kittery Point, Me./Aug. '91/no. 285"). I have declined to designate a lectotype because of the good possibility that this former series was not in Emery's hands at the time of original description, but there can be no doubt that the name has been correctly placed.

DISTRIBUTION. This species is evidently limited to eastern North America. Following are all of the records accumulated during the present study. NOVA SCOTIA: Pleasantfield (W. H. Prest leg.; MCZ). MAINE: Kittery Point (syntypes from Emery Coll.). NEW HAMPSHIRE: East Jaffrey (R. E. Dan-

forth leg.; MCZ). MASSACHUSETTS: Forest Hills, winged queens and males VIII-12-1910 (M. Tanquary leg.; MCZ); Stony Brook Reservation (W. S. Creighton leg. and Coll.); Lexington, dealate queen VI-22-1953 (R. H. Lippitt leg.; MCZ); Springfield (MCZ); Natick, winged queen IX-20-1923 (MCZ). CONNECTICUT: Colebrook (W. M. Wheeler leg., MCZ). NEW YORK: Flushing (K. W. Cooper leg.; MCZ). NEW JERSEY: Caldwell, Essex Co. (USNM). PENNSYLVANIA: Oxford, Chester Co., and Ottsville, Bucks Co. (W. L. Brown leg.; Pennsylvania State University Collection). INDIANA: Steuben Co. (R. L. Morris leg.; USNM). OHIO: Holland, Lucas Co., male VIII-20?-1932 (M. Talbot leg. and Coll., MCZ). ILLINOIS: Volo, Lake Co. (Talbot leg. and Coll., MCZ); Wauconda, Lake Co. (Ross and Sanderson leg.; INHS); Antioch, Lake Co. (Ross and Sanderson leg.; INHS); Chicago (MCZ); Rockford (MCZ). MICHIGAN: Livingston Co. (Talbot leg. and Coll., MCZ). MINNESOTA: Hennepin Co. (C. T. Schmidt leg.; USNM). VIRGINIA: Vienna, Fairfax Co. (J. C. Bridwell leg.; USNM).

ECOLOGY. Notes accompanying the above records indicate that *minutus* prefers to nest in sphagnum bogs and swampy meadows but will also move into open, dry forest. It has been taken most often in mounds or masonry domes in open areas, and only once (Steuben Co., Ind.) in a log. Brown (pers. commun.) has supplied me with complete notes on his Pennsylvania collections. South of Oxford, near the Pennsylvania-Maryland border, he found a population of this species nesting in masonry domes on the open grassy floor of a tongue of pitch pine woods. These domes measured between about 8 and 18 inches in height and about 2 feet in base diameter, had peculiar bulging sides, and were overgrown with short grass. Similar domes were found in a population at Ottsville along the border of an old pasture and oak-hickory woods. At both localities workers were rather scarce in the nests, and at Ottsville some of the domes were inhabited by *Formica fusca* instead.

A clue to the host species of *minutus* is supplied by the following note accompanying a series in the United States National Museum: "N. J./Aug. 15 '85/in hickory stem with L. alienus." The nesting site is one typical for *alienus*, and the determination in this case was probably correct.

LASIUS BICORNIS (Foerster)
(Subg. *Chthonolasius*)

Formica bicornis Foerster, 1850, Hymenopterologische Studien, no. 1, pp. 41–43; queen; original description. Type locality: Aachen, Germany.

Lasius bicornis oertzeni Forel, 1910, Ann. Soc. Ent. Belg., **54**: 26–27; worker, queen, male; original description. Type locality: Peloponnesus, Greece. NEW SYNONYMY.

Lasius oertzeni, Stärcke, 1937, Tijdschr. Ent., **80**: 56.

Formicina microgyna Bondroit, 1918, Ann. Soc. Ent. Fr., **87**: 33–34; queen, male; original description. Type locality: Saint Affrique, Aveyron, France, by present selection. NEW SYNONYMY.

Lasius bicornis var. *neapolitana* Emery, 1922, Bull. Soc. Ent. Ital., **54**: 13; queen, male; original description. Type locality: Naples, Italy. NEW SYNONYMY.

Acanthomyops bicornis kashmirensis Donisthorpe, 1930, Ann. Mag. Nat. Hist., (10) **5**: 225–226; queen, male; original description. Type locality: Kashmir. NEW SYNONYMY.

DIAGNOSIS. A rare Eurasian species somewhat similar in habitus to the North American species *minutus* but showing profound differences in the petiolar outline and pilosity. The following diagnosis is based on part of the type series of *oertzeni* and *microgyna* (including specimens labelled as syntypes of *microgyna* but coming from Saint Sever, Aveyron, a locality not mentioned in the original description), on a single unlabelled worker from the Mayr Collection, and on descriptions and figures (by Dr. H. Bischoff) of two queens in the Berlin Museum.

Queen. (1) Smaller than *umbratus* but considerably larger than *minutus*. HW of *oertzeni* lectotype 1.34 mm.; *microgyna* lectotype 1.25 mm., syntopotypes 1.24 and 1.26 mm., Saint Sever "syntypes" 1.22 and 1.29 mm.; a queen from the Taurus Mountains, Turkey (Berlin Museum), 1.34 mm. (measured by H. Bischoff).

(2) Long standing hairs abundant over the alitrunk, approaching the *minutus* condition, but sparser on the head and gastric tergites. In full face, the number of hairs projecting beyond the occipital contour is 4 in the *oertzeni* lectotype, 6 in the *microgyna* lectotype, 5 and 7 in the *microgyna* syntopotypes, and 6 and 7 in the Saint Sever specimens; the number in *minutus* is commonly 30 or more. In perfect side view, the first gastric tergite of the *oertzeni* lectotype shows only 15 standing hairs

projecting beyond its profile, the *microgyna* lectotype 12, and *microgyna* syntopotypes 10 and 14, the St. Sever specimens 13 and 15, and a specimen from Hanau (Berlin Museum) 7; the typical number for *minutus* is 25 or more. In *bicornis* the pilosity of the first gastric tergite is limited mostly to the anterior slope and extreme posterior strip; in *minutus* it is evenly distributed over all of the tergital surface except for the anteriormost part of the anterior slope. The body hairs are proportionately shorter than in *minutus*. The longest hairs of the first and second gastric segments shorter than the maximum width of the hind tibia at its midlength (in the *oertzeni* lectotype, for instance, maximum hair length is 0.17 mm., tibia width is 0.21 mm.). At the same time, *bicornis* resembles *minutus* in having the scapes and legs completely bare of hairs except for a few scattered along the flexor margins of the femora.

(3) The petiole in frontal view slender, tapering dorsally; deeply emarginate, so that the depth of the emargination measured from the level of the bicornuate dorsal crest to the bottom of the emargination is distinctly greater than the width of the emargination taken across the midpoint of the depth measurement (Pl. 2, Fig. 2).

(4) Scapes flattened as in *rabaudi;* in the *oertzeni* lectotype, the maximum width at the midpoint is 0.14 mm., the minimum width only 0.07 mm. At the same time, the funicular segments are not elongated as in *rabaudi;* third funicular segment length in *oertzeni* lectotype 0.11 mm., width 0.10 mm.

(5) As in *minutus*, the mandibles more massive relative to the remainder of the head and set farther apart from the midline when compared with *umbratus*.

Worker. (Based on a single *oertzeni* syntype and an unlabelled worker in the Mayr Collection). (1) PW of *oertzeni* syntype 0.68 mm., Mayr specimen 0.79 mm., well within range of *umbratus* size variation.

(2) Body hair longer than in *umbratus-rabaudi* but shorter and finer than in *minutus*. In both available specimens the dorsal gastric hairs average about 0.09 mm. and do not exceed 0.14 mm.; the maximum width of the hind tibia at its midlength commonly used in the present study as a reference measurement, is 0.16 mm. The cephalic and gastric hairs of these specimens are sparser than in *minutus*. The number of hairs extending

beyond the profile of the first gastric segment anterior to the extreme posterior strip and seen in perfect side view is 17 in the *oertzeni* syntype and only 6 in the Mayr specimen; 30 or more is usual for *minutus, umbratus-rabaudi,* and *subumbratus.*

(3) Petiolar outline in the *oertzeni* syntype similar to that described for the queen (Pl. 2, Fig. 3); emargination somewhat more shallow in the Mayr specimen.

(4) Scape flattened to the extent seen in extreme *rabaudi* workers. *Oertzeni* syntype: maximum width at scape midlength 0.11 mm., minimum width 0.06 mm. Mayr specimen; maximum width 0.12 mm., minimum width 0.07 mm.

HOLOTYPE. Dr. Bischoff has informed me that the unique type of *bicornis* is not with the Foerster Collection in the Berlin Museum, and it has not been found among the Foerster material in the Mayr Collection. Fortunately, the original description adequately covers the essential diagnostic features in petiole shape and pilosity of this distinctive species, and there can be little doubt that the name has been correctly applied in the present study.

SYNONYMY. The type series of *Lasius bicornis oertzeni* Forel and *Formicina microgyna* Bondroit are nearly identical with one another, as demonstrated in the preceding descriptions. Lectotypes have been selected herein and returned to the collections of the original describers.

Lasius bicornis var. *neapolitana* Emery, as represented in the original description, is separable from *microgyna* only by a trivial difference in the depth of the occipital concavity.

The original description of *Lasius bicornis kashmirensis* Donisthorpe is unfortunately vague, but Donisthorpe does mention two diagnostic characters which seem to place it definitely with this species: (1) the gastric pilosity is very sparse, (2) the petiolar scale matches, with slight differences, that of *neapolitana.* Since *bicornis* is such a distinctive species, I have proposed tentative synonymy for *kashmirensis* as preferable to leaving it a *nomen dubium.*

LASIUS HUMILIS Wheeler
(Subg. *Chthonolasius*)

Lasius humilis Wheeler, 1917, Proc. Amer. Acad. Arts Sci. Boston, 52: 528; worker, queen; original description. Type locality: Pyramid Lake, Nevada.

DIAGNOSIS. A small, pale-colored species known only from a limited area in the southwestern United States.

Queen. (1) The smallest North American *Chthonolasius* known; HW of the three syntype queens measured 1.04, 1.06, and 1.06 mm. respectively.

(2) Scapes longer relative to head width than in any other small *Chthonolasius;* SI of syntypes 85, 88 and 90 respectively, whereas in *umbratus, rabaudi, minutus,* and *bicornis* SI probably never exceeds 82 or 83 and is usually less than 80.

(3) Standing hairs absent from the appendages and sparse on the body. Seen in full face, no more than one or two standing hairs project beyond the entire cephalic contour posterior to the mandibular insertions. Gastric pilosity short and fine; gastric pubescence abundant and completely appressed.

(4) Body and appendages medium yellow, the occiput and thoracic dorsum lightly infuscate.

Worker. This caste by itself may at first be confused with nanitic workers of *L. umbratus*, but differs in the obliteration of the promesonotal impression and in the unusual petiole shape.

(1) Very small; extreme PW range of all series examined 0.53-0.63 mm.

(2) Promesonotal impression seen in side view very feeble or lacking.

(3) Eyes small relative to head; EL range 0.12-0.15 mm.

(4) Dorsal crest of the petiole in frontal view wedge-shaped, tapering upward to form an angular, non-emarginate median prominence.

(5) Body color uniformly light yellow.

LECTOTYPE. By present selection, a queen in the Museum of Comparative Zoology labelled "Pyramid Lake, Nev. W. M. Mann." HW 1.04 mm. Additional syntype queens and workers are in the Museum of Comparative Zoology. A queen and two workers in the T. W. Cook Collection are probably also part of the original type series, despite their differing label "Pyramid Lake, Nev. 4-6-45."

DISTRIBUTION. Series from the following localities have been examined during the present study. NEVADA: Pyramid Lake (type series). COLORADO: Salida (W. M. Wheeler leg.; MCZ); 10 miles south of Trinidad, 6500 feet (A. C. Cole leg. and

Coll., MCZ). NEW MEXICO: Tesuque Canyon, Hyde State Park, near Santa Fe, 8700 feet (Cole leg. and Coll., MCZ).

ECOLOGY. Dr. Cole (*in litt.*) has kindly supplied me with the following notes on his Colorado and New Mexico collections. The Trinidad, Colo., colony was found under a stone in the moist soil of a mountain meadow. The Tesuque Canyon, N. Mex., colony was found under a stone in moist, open pine-aspen woods.

Lasius crinitus (F. Smith)
(Subg. *Chthonolasius*)

Formica crinita F. Smith, 1858, Cat. Hym. Brit. Mus., **6**: 13; queen; original description. Type locality: northern India.

Lasius crinitus, Bingham, 1903, The Fauna of British India (Taylor and Francis, London), Hym., **2**: 339–340. (Further description of the holotype.)

Acanthomyops hingstoni Donisthorpe, 1929, Ann. Mag. Nat. Hist., (10) **4**: 448–449; worker; original description. Type locality: Darjeeling, India. NEW SYNONYMY.

DIAGNOSIS. A large, aberrant species known only from the Himalayas. The following diagnosis is based on a single alate queen from Sikkim and three syntype workers of *hingstoni* (all MCZ).

Queen. (1) Largest *Lasius* known; HW of Sikkim queen 1.99 mm.

(2) Pilosity of alitrunk and gaster consisting of extremely long, fine, sinuous, predominantly appressed yellow hairs, which are concentrated along the posterior margin of the pronotum, lateral faces of the scutum, lateral and ventral sides of the first two gastric segments, frontal declivity of the first gastric tergite, and whole surfaces of the exposed posterior gastric segments. They are especially abundant on the posterior gastric segments, converging to form a matted sheath over the apex, but they are sparse over most of the dorsal surfaces of the first two gastric segments and the scutum, and absent altogether from the appendages, the head, most of the pronotum, and all of the propodeum. Similar hairs, many doubled over and wicket-shaped, form a dense fringe along the dorsal crest of the petiole. Shorter, mostly non-sinuous hairs occur on the mandibles and around

the metapleural gland openings. The single specimen examined (Sikkim) is rather badly battered and probably has had some hairs worn off, but its pilosity pattern still agrees generally with that described by Bingham for the holotype.

(3) Scape moderately flattened; in the Sikkim specimen, maximum width at midlength 0.15 mm., minimum width 0.12 mm.

(4) Gastric tergites with abundant appressed pubescence.

(5) Body uniformly ochraceous, the appendages somewhat lighter. The entire body, including the gastric tergites, shagreened and feebly shining to subopaque.

(6) Petiole in frontal view with broadly rounded dorsolateral corners, converging toward the midline to meet a narrow, obtusely angular median excision.

Worker. On the basis of its size, pilosity, petiole shape, and geographic origin, Donisthorpe's species *hingstoni* is considered herein the worker caste of *crinitus.* Three of Donisthorpe's syntypes were used in the following diagnosis.

(1) Exceptionally large; PW 0.88, 0.90, and 0.93 mm. respectively.

(2) Dorsal crest of petiole seen in frontal view wedge-shaped, its sides tapering upward to form an angular, non-emarginate median prominence.

(3) Body pilosity consisting of long, coarse, suberect-erect hairs; maximum length on first two gastric tergites 0.18 mm., on pronotum 0.21 mm., on occiput 0.23 mm. These hairs are concentrated mainly on the occipital margin, pronotum, posterior third of the mesonotum, dorsal convexity of the propodeum, dorsal crest of the petiole, and entire gastric surface; they are occasional over the anterior surface of the head. Appendages completely lacking outstanding pilosity except for a few short, erect hairs on the coxae.

(4) Scapes somewhat flattened, maximum width at midlength 0.13 mm., minimum width 0.08 mm.

(5) Contrary to Donisthorpe's statement, the maxillary palps are not five-jointed, but six-jointed as in other species of *Lasius.*

HOLOTYPE. A queen in the British Museum. From Bingham's detailed description there can be no question about the identity of this exceptional species.

Lasius carniolicus Mayr
(Subg. *Chthonolasius*)

Lasius carniolicus Mayr, 1861, Europäischen Formiciden (Ameisen), p. 51; queen; original description. Type locality: Laibach, Yugoslavia.

Lasius carniolicus var. *kusnezovi* Karawajew, 1929, Acad. Sci. Ukraine, Mem. Sci. Phys. Math., **13:** 212–213, fig. 5; worker; original description. Type locality: Dau Baba Mountains, Chimkent District, Kazakh S. S. R., Soviet Central Asia. NEW SYNONYMY.

DIAGNOSIS. *Queen.* (1) The smallest of all the species of *Lasius* in this caste, not exceeding in total size the worker caste; HW of 5 specimens examined (from 5 localities) 0.76, 0.77, 0.77, 0.77, 0.78 mm.

(2) Petiole seen from the side shaped like an inverted U: short, thick, and broadly convex dorsally. In frontal view the dorsal crest broadly convex and non-emarginate. (Pl. 2, Fig. 5).

(3) Mandible relatively small, slender, and delicate, subfalcate with a concave masticatory border and prominent long, narrow apical tooth. Dentition reduced to the apical, subapical, first intercalary, and three basal teeth.

(4) Entire body covered with light yellow standing hairs which rarely exceed 0.11 mm. in length. These are unusual in being abundant over the gular surface and around the entire cephalic margin. Shorter hairs, predominantly decumbent-subdecumbent, occur over all surfaces of the femora and tibiae. Body pubescence everywhere dense, long, and predominantly appressed.

(5) Wings hyaline, unlike those of other *Chthonolasius,* and exceptionally long proportional to the body size (wing length exceeding 4.5 mm.).

(6) Body uniformly medium brown, appendages yellowish brown.

Worker. (1) Petiole seen from the side thick, with a broadly rounded dorsal crest; in frontal view gently tapering dorsally, the dorsal crest convex and non-emarginate.

(2) Eyes set in shallow circumocular depressions and quite small relative to head size; EL 0.11-0.13 mm.

(3) Mandibles more slender than in other *Lasius,* with a reduced offset basal tooth as in *L. sitkaensis.*

(4) The mandibles set closer to the median line than in

other *Lasius;* in frontal view the genal margins (from the anterior borders of the eyes to the mandibular insertions) strongly convex.

(5) Body hairs relatively short and sparse, those on the first three gastric tergites predominantly decumbent. Appendages nearly devoid of pilosity, with only an occasional short decumbent hair along the flexor margins. Body and appendage pubescence dense and predominantly appressed.

(6) Body and appendages medium yellow to very light brownish yellow, the median and posterior areas of the head usually somewhat darker, medium to dark yellowish brown.

(7) Size apparently averaging smaller than in most *Chthonolasius;* extreme PW range of sample studied 0.53-0.60 mm.

Male. (1) Lateral profile of petiole as in worker; in frontal view the dorsal margin is flat to feebly emarginate.

(2) Size small for *Chthonolasius;* HW of single specimen measured 0.83 mm.

(3) Mandibles with numerous irregular denticles along the entire length of the masticatory border.

(4) Moderately long hairs (not exceeding 0.13 mm. in length) abundant over the entire body, including the gular surface and all of the cephalic margin posterior to the eyes. The hairs of the head and alitrunk predominantly suberect-erect, those on the gaster predominantly decumbent. Scapes and tibiae lacking outstanding pilosity; the femora with fairly numerous short standing hairs.

(5) Subgenital plate of the single male dissected differing from that of other *Chthonolasius* in having a relatively straight posterior border, the posterolateral corners not projecting posteriorly. The median posterior setiferous area feebly convex and bearing 6 irregularly placed hairs. The cuspis of the volsella unusually thick, its greatest width exceeding the greatest width of the digitus.

HOLOTYPE. The unique type is in the Mayr Collection. A metatopotype queen borrowed from this collection is typical of the population and has been employed with other specimens in making the above diagnosis.

DISTRIBUTION. *Carniolicus* is widely distributed through most of the Palaearctic Region, although it has never been taken in Japan, England, or North Africa. Following are the records

verified during the present study. FRANCE: Drôme, winged queens and males X-1921 (A. Forel leg.; MCZ). SWITZERLAND: Lägern, winged queens X-13-1945 (Kutter Coll., USNM); Monte Generoso (W. M. Wheeler leg.; MCZ); Locarno (Wheeler leg.; MCZ). POLAND: Mosor (D. Müller leg.; MCZ). YUGOSLAVIA: Laibach (Mayr Coll.). KAZAKH S.S.R.: Duany Tau Mountains (N. Kusnezov leg.; MCZ).

The following additional records have been published by previous authors and are probably reliable: Miramount-de-Quercy, France (Vandel, 1926); Visby, Gotland (Forel, 1908); Ponta di Classe, Romagna, Italy (Consani and Zangheri, 1952); Capraia Island, Italy, queen X-1927 (Finzi, 1933); Askole, Karakoram, 3000 meters (Menozzi, 1939). In a distribution map published in 1929 (a), Kuznetzov-Ugamskij indicates records from the following Soviet localities: Kazan; near Sterlitamak in the Urals; the central Caucasus; Abakan, Khakass; the southern Yablonovy Mountains, Chita; Nikolsk-Ussurijsk, Maritime Territory.

ECOLOGY. This species apparently holds its nuptial flights late in the year, since all of the reproductives recorded so far have been collected in October. Kutter (1946) mentions a nuptial flight which occurred at Lägern, near Zurich, at 4 p.m., October 13.

SYNONYMY. *Lasius carniolicus* var. *kusnezovi* Karawajew. This variety, described without direct comparison to specimens of "typical" *carniolicus*, is said to differ by its smaller size, lighter color, and slightly different head shape (less convex genal borders, more convex anterior clypeal border). The first two characters apply to structures which are highly variable in the European population, and on the basis of the description alone they cannot be considered to have taxonomic significance. Judging from Karawajew's figures, the anterior border of the median clypeal lobe of *kusnezovi* is somewhat narrower and the genal borders less convex than in any of the series I have studied, and may be meaningful. Yet the differences seem to fade when compared with the really profound characters which distinguish *carniolicus* as a species. Moreover, the Duany Tau Mountains series, taken in the same general area as *kusnezovi*, shows no significant difference from European series, and Menozzi (1939)

could find no differences in his Karakoram material, thus practically eliminating the possibility of *kusnezovi* representing a geographic trend in the Asian population.

Species properly excluded from Lasius

Acanthomyops edwardsi Donisthorpe, 1933, Ann. Mag. Nat. Hist., (10) **12:** 535.

Acanthomyops negrensis Donisthorpe, *ibid.*, p. 537.

Acanthomyops rufo-niger Donisthorpe, *idem*, p. 537.

These three species, originating from Argentina, have already been transferred as synonyms of well known species in the melophorine genus *Lasiophanes* (Kusnezov, 1951).

Lasius eskamole Reza, 1914, Mem. Rev. Soc. Cient. "Antonio Alzate" (Mexico City), **44:** 1–22.

The description of this species with the attendant biological notes is nearly unintelligible. Although it may be impossible ever to place *eskamole* to the correct genus (Reza's crude figures are vaguely reminiscent of *Camponotus*), at least it is safe to say that it is not a *Lasius*.

Nomina dubia

The following two species were originally described in *Lasius* but could not be identified on the basis of available descriptions and material.

Lasius terreus Scudder, 1878, Bull. U. S. Geol. Geogr. Surv. Terr., **4:** 747–748; worker; original description. Also, 1890, Bull. U. S. Geol. Surv. Terr., **13:** 618; pl. 10, fig. 23.

(*Formicidae*) *terreus*, Carpenter, 1930, Bull. Mus. Comp. Zool., **70:** 19.

This species was described from the Green River shales of Wyoming (middle Eocene). According to Carpenter, the unique type is too poorly preserved to allow generic placement.

Acanthomyops (*Donisthorpea*) *kosswigi* Donisthorpe, 1950, Ann. Mag. Nat. Hist., (12) **3:** 638; worker, queen; original description. Type locality: Kars, Turkey. Location of types: British Museum (Natural History).

Donisthorpe's description contains nothing which even hints at the relationship of this species to other members of the genus. Until the types can be examined again, even the subgeneric placement will remain a guess.

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INDEX

Ant Genus *Lasius*

[1] *Lasius* (*Formicina*) *flavus claripennis* Wheeler, 1917, Proc. Amer. Acad. Arts Sci., 52:527, worker, female, male. Synonymized with *L. flavus microps* Wheeler by Creighton, 1950, p. 422.

PLATE 1

Fig. 1. Mandibles and clypeus of *L. sitkaensis* worker (composite).

Fig. 2. Mandibles and clypeus of *L. niger* complex worker (composite).

Fig. 3. Mandibles and clypeus of *L. neoniger* complex worker (composite).

Fig. 4. Right mandible of *L. sitkaensis* male (Golden Valley Co., N. Dak.), camera lucida outline, illustrating the "*sitkaensis* type" mandible.

Fig. 5. Right mandible of *L. alienus* male (Abercrombie, Richland Co., N. Dak.), camera lucida outline, illustrating the "*niger* type" mandible.

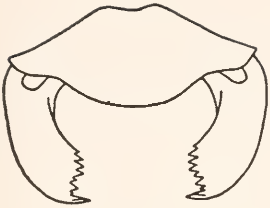
Fig. 6. Head of *L. niger* minima worker (Lausanne, Switzerland, from an incipient colony reared by M. Bibikoff).

Fig. 7. Head of *L. niger* medium-sized worker (Peking, China; HW 1.04 mm.).

Fig. 8. Head of *L. emarginatus* medium-sized worker (Cremona, Italy).

Fig. 9. Head of *L. brunneus* medium-sized worker (Berks, England).

(Figs. 1–5 drawn to a larger scale than Figs. 6–9.)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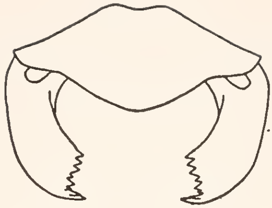
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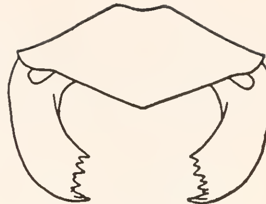
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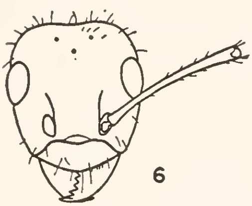
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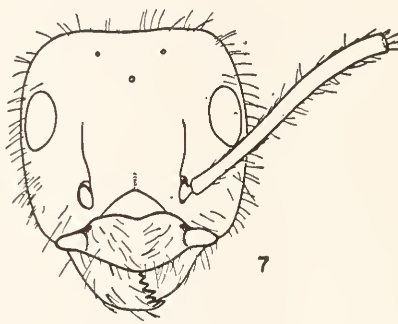
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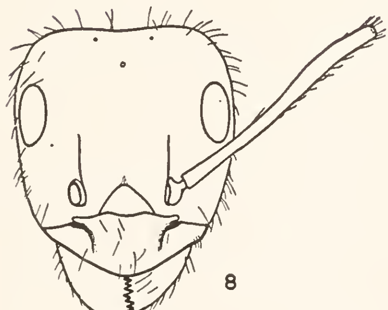
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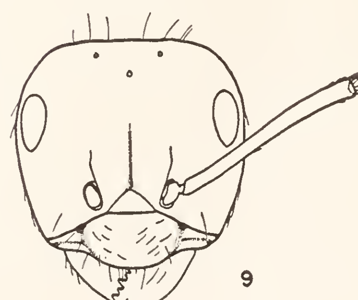
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PLATE 1

PLATE 2

Fig. 1. Rear view of petiole of *L. umbratus* queen, showing the maximum amount of dorsal emargination attained by that species. Drawn from a putative *Formica affinis* Schenck syntype; see further explanation in text. Maximum petiole width 0.55 mm.

Fig. 2. Rear view of petiole of *L. bicornis* queen. Drawn from lectotype of *L. oertzeni* Forel, a junior synonym.

Fig. 3. Rear view of petiole of *L. bicornis* worker. Drawn from a *L. oertzeni* synnidotype.

Fig. 4. Rear view of petiole of *L. minutus* worker. Drawn from a syntype from Kittery Point, Maine.

Fig. 5. Rear and right side views of petiole of *L. carniolicus* queen. Drawn from a metatopotype.

Fig. 6. Right side view of petiole of *L. spathepus* worker (Odawara, Japan).

Fig. 7. Right side view of petiole of *L. fuliginosus* worker (Odawara, Japan).

Fig. 8. Right side view of petiole of *L. crispus* worker (syntype from central Korea).

Fig. 9. Subgenital plate of *L. fuliginosus* (Odawara, Japan).

Fig. 10. Subgenital plate of *L. spathepus* (Odawara, Japan).

Fig. 11. Right pygostyle of *L. fuliginosus* (Odawara, Japan), illustrating the form characterizing this species as well as the subgenera *Lasius* and *Cautolasius*. Pilosity not shown.

Fig. 12. Right pygostyle of *L. spathepus* (Odawara, Japan), illustrating the form characterizing this species as well as the subgenus *Chthonolasius*. Pilosity not shown.

Fig. 13. Variation in form of the male maxillary palp in a single nest series of *L. fuliginosus* (Odawara, Japan), showing the variable ankylosis characterizing the subgenus *Dendrolasius*. The top palp shows the unusual condition of a full complement of six segments; the middle palp has five segments (V and VI fused); and the bottom palp has five segments with no. IV greatly diminished. The middle and bottom palps are from the same individual.

(All figures by camera lucida and approximately to scale).

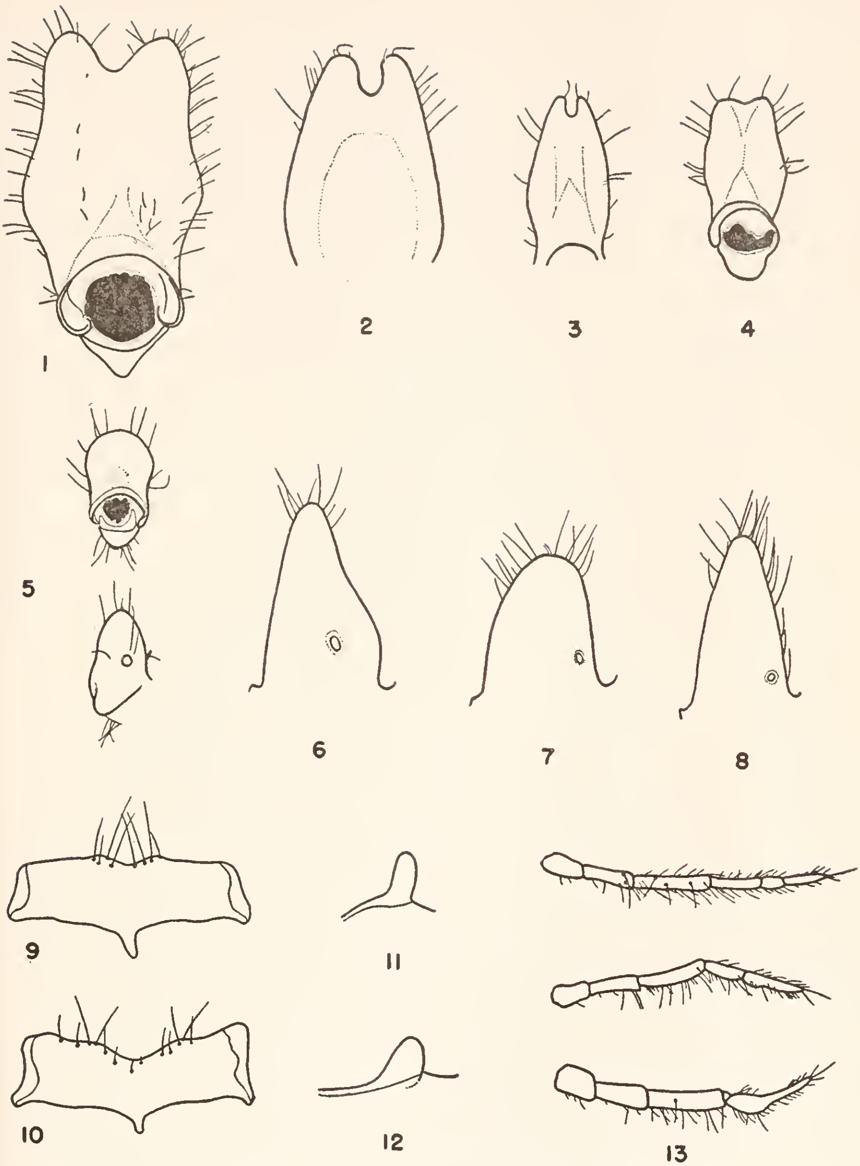

PLATE 2

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 113, No.2

OCCURRENCE OFF THE MIDDLE AND NORTH ATLANTIC UNITED STATES OF THE OFFSHORE HAKE *MERLUCCIUS ALBIDUS* (MITCHILL) 1818, AND OF THE BLUE WHITING *GADUS (MICROMESISTIUS) POUTASSOU* (RISSO) 1826

BY HENRY B. BIGELOW AND WILLIAM C. SCHROEDER

Museum of Comparative Zoology and
Woods Hole Oceanographic Institution

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PRINTED FOR THE MUSEUM
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No. 2.—*Occurrence off the Middle and North Atlantic United States of the Offshore Hake Merluccius albidus (Mitchill) 1818, and of the Blue Whiting Gadus (Micromesistius) poutassou (Risso) 1826*[1]

By Henry B. Bigelow and William C. Schroeder

INTRODUCTION

Among the more interesting of the bony fishes trawled by the dragger "Cap'n Bill II," from the Woods Hole Oceanographic Institution, in deep water between the offings of Virginia and of middle Nova Scotia in 1952 and 1953 (Bigelow and Schroeder, 1954, p. 39), were many specimens of the western Atlantic representative of the European silver hake *Merluccius merluccius,* recently described by Ginsburg (1954, p. 192) under the specific name *albidus* Mitchill 1818, and four specimens of the blue whiting *Gadus* (*Micromesistius*) *poutassou* (Risso) 1826, which has not been reported before from the western side of the Atlantic.

OFFSHORE HAKE

Merluccius[2] albidus (Mitchill) 1818

It had been taken for granted, until very recently, that the hordes of silver hake or whiting inhabiting the continental waters of the western Atlantic from New Jersey to the outer coast of Nova Scotia all belonged to the one species *Merluccius bilinearis* (Mitchill) 1814. But it has developed, of late, that the *Merluccius* populations over the outer part of the continental shelf, and along the upper belt of the continental slope also include a second member of the genus that is more nearly related to the hake of northern European seas (*Merluccius merluccius* Linnaeus 1758), but differing sufficiently from the latter to deserve recognition as a separate species.

Our own first hint of this was the discovery that the sample that was retained from the "Cap'n Bill II" trawlings of 1952 fell into two categories, the one with the numbers of anal fin rays (39-41), of scales (103-110), and of gill rakers (16-20) that characterize *M. bilinearis*, the other group with fewer anal

1 Contribution No. 732 from the Woods Hole Oceanographic Institution.

2 The so-called silver hakes have been referred for many years to the genus *Merluccius* of Rafinesque 1810. According to Whitley (1948, p. 83) this name is equivalent to *Merlangius* Geoffroy 1767 (vol. 5, p. 401, pl. 661), hence should be replaced by the latter. But the heading to Geoffroy's description of his *Merlangius* included only this one name; i.e. it was not binomial. And in any case his illustration of it, showing three separate dorsal fins, seems to have been of the European whiting *Gadus merlangus* Linnaeus 1758. Indeed, the caption ("Merlangius, Merlan") indicates as much, for merlan is the common French name for that fish. We owe to the library of the Arnold Arboretum our opportunity to consult Geoffroy's work.

rays (36-39), and fewer (9-11) gill rakers (Fig. 1), but a larger number of scales (132-148) as is the case in *M. merluccius.* Armed with this knowledge, the 2962 silver hakes that were taken in 1953 were examined in these respects, with the result that while 535 of them proved to be typical *bilinearis,* 2427 of them yielded the counts that had been credited to *M. merluccius* in published accounts of the latter. And comparison between these "Cap'n Bill II" specimens and 20 *M. merluccius,* 360-595 mm. long (14 of them from Plymouth, England, 6 of them from Portugal, received through the kindness of Dr. F. S. Russell and Dr. A. M. Ramalho) has confirmed their unity in these respects.

This result is in line with Ginsburg's (1954) recent announcement that the U. S. National Museum's collection of silver hakes from the east coast of the United States — presumably all *M.*

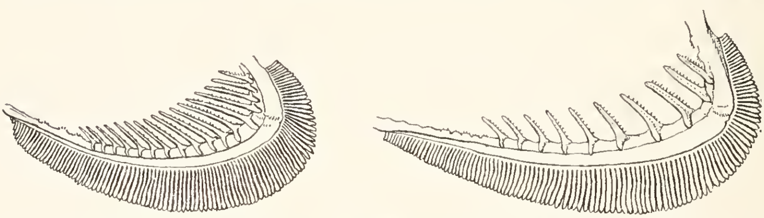

Fig. 1. Right, first gill arch from *Merluccius albidus* 368 mm. long, and left, from *Merluccius bilinearis* 331 mm. long, about 0.9x.

bilinearis — also includes representatives of a second form that resembles *M. merluccius* more closely than it resembles *bilinearis,* and which (from his excellent account) we judge to be identical with the "Cap'n Bill II" series of *M. merluccius* affinity.

Ginsburg described this hake as a species distinct from *M. merluccius* under the name *albidus* Mitchill 1818, with pectoral fins consistently a little longer, number of 1st dorsal fin rays ranging larger by about one, and number of scales ranging lower in the western Atlantic population than in the eastern Atlantic (for details, see Tables I, II, also Ginsburg, 1954, p. 193). These differences justify his specific separation of the one from the other. We refer the reader to Ginsburg, 1954, page 194 [1] for the reasons for applying the old name *albidus* to the western Atlantic form, in preference to coining a new specific name for it.

[1] The early nomenclatural history of the genus *Merluccius* in northeastern American waters is a confused one.

TABLE I. *Merluccius merluccius* and *M. albidus*

Species		*M. merluccius*	*M. merluccius*	*M. albidus*
Locality		Plymouth, England	Lisbon, Portugal	off New England
Number of specimens		14[1]	6[2]	14
Total length	mm.	277-595	353-363	300-590
Standard length	mm.	249-540	318-327	272-539
Eye, horizontal	percent of head	13.8-19.9	18.4-20.7	17.7-21.0
Snout	percent of head	31.1-40.2	30.3-33.7	28.2-36.3
Head	percent of S.L.	26.5-30.3	27.6-29.8	27.5-30.3
1st dorsal, base	percent of S.L.	8.7-10.5	8.9-10.2	9.1-12.3
Pectoral, length	percent of S.L.	15.9-17.6	15.7-17.6	17.6-21.2
Pelvic, length	percent of S.L.	13.7-17.0	15.0-16.5	12.1-17.6
1st dorsal, rays	number	9-11	9-10	11-12
2nd dorsal, rays	number	37-40	37-39	36-40
Anal, rays	number	36-39	36-39	36-39
Pectoral rays	number	14-15	14-15	14-15
Pelvic rays	number	7	7	7
Scales	number	152-170	163-180	132-148
Gill rakers, 1st arch	number	9-11	9-11	9-11
Gill rakers, longest	percent of eye length	40.7-57.0	35.8-47.0	41.4-54.5

1 Kindly contributed by Dr. F. S. Russell.
2 Kindly contributed by Dr. A. M. Ramalho.

The "Cap'n Bill II" specimens of *albidus* were from 4 to 28 inches in total length, thus covering the range from yearlings to adults perhaps 9-10 years old, if their rate of growth is about the same as it is for *M. merluccius* off Ireland (Belloc, 1929). And the presence of ovaries nearing ripeness in large females of *albidus* taken off Virginia, off Long Island, New York, and off Martha's Vineyard, June 26 and 29, 1953 and July 7, 1954,

TABLE II

1st dorsal rays, Number	*M. merluccius* Specimens	*M. albidus* Specimens
9	6	
10	13	
11	1	8
12		6
Pectoral rays, Number	Specimens	Specimens
14	18	2
15	2	12
Scales Number	Specimens	Specimens
131-140		10
141-150		4
151-160	6	
161-170	11	
171-180	3	
Pectoral length in percent of S.L.	Specimens	Specimens
15.7-16.0	3	
16.1-17.0	13	
17.1-18.0	4	3
18.1-19.0		1
19.1-20.0		4
20.1-21.0		5
21.1-21.2		1

is evidence that the large adults, at least, are midsummer spawners. The stomach contents of the specimens opened consisted chiefly of black pelagic fishes, mostly myctophids, with snipe eels (*Nemichthys*) and squids. And many myctophids were disgorged by the larger of the hakes, enough in fact on one occasion to make the deck slippery. Thus their feeding habits correspond to those of the European *M. merluccius* (p. 212).

The 37 stations where "Cap'n Bill II" took *albidus* in the summer of 1953 were distributed from the southeastern slope of Georges Bank (Lat. 40°46′N; Long. 66°48′W) to the most southerly haul off Virginia (Lat. 37°38′N, Long. 74°15′W) without evident concentration within any particular sector. And in the summer of 1954 it was taken by "Atlantis" at 10 stations between Lat. 40°47′N, Long. 66°40′W and Lat. 39°54′N, Long. 70°47′W. This is in line with Ginsburg's (1954, p. 193) published report of *albidus* from various localities between the southwestern part of Georges Bank and the offing of Cape Henry, Virginia (Fig. 2). The list of localities whence it is represented in the collection of the U. S. National Museum (information contributed by letter from Dr. Ginsburg) also includes the offings of Savannah, Georgia, and Cape Canaveral, Florida. And a probable record from Tortugas, Florida, (Ginsburg 1954, p. 193) suggests that its geographic range is continuous around Florida with that of the new species *magnoculus* recently described by Ginsburg (1954, p. 194) from the Gulf of Mexico. We suspect, however, that the center of population for *albidus* lies off the middle Atlantic coast, for silver hakes of whichever species are not caught in commercial quantities south of Chesapeake Bay; very few in fact, southward beyond New Jersey (landings, 1951: New England 118,466,000 pounds; New York 684,000 pounds; New Jersey 897,000 pounds; Maryland 11,200 pounds; Virginia 17,200 pounds).

Failure to pick up even a single *albidus* in any of the successful hauls that were made by "Cap'n Bill II" at appropriate depths along the Nova Scotian shelf and slope in 1953, though 5 hauls did take a few *bilinearis*, suggests that *albidus* did not range eastward beyond Georges Bank at the time. And even if it should prove to occur as far as the Newfoundland Banks in that direction, as *bilinearis* does, the geographic range of *M. albidus* in the

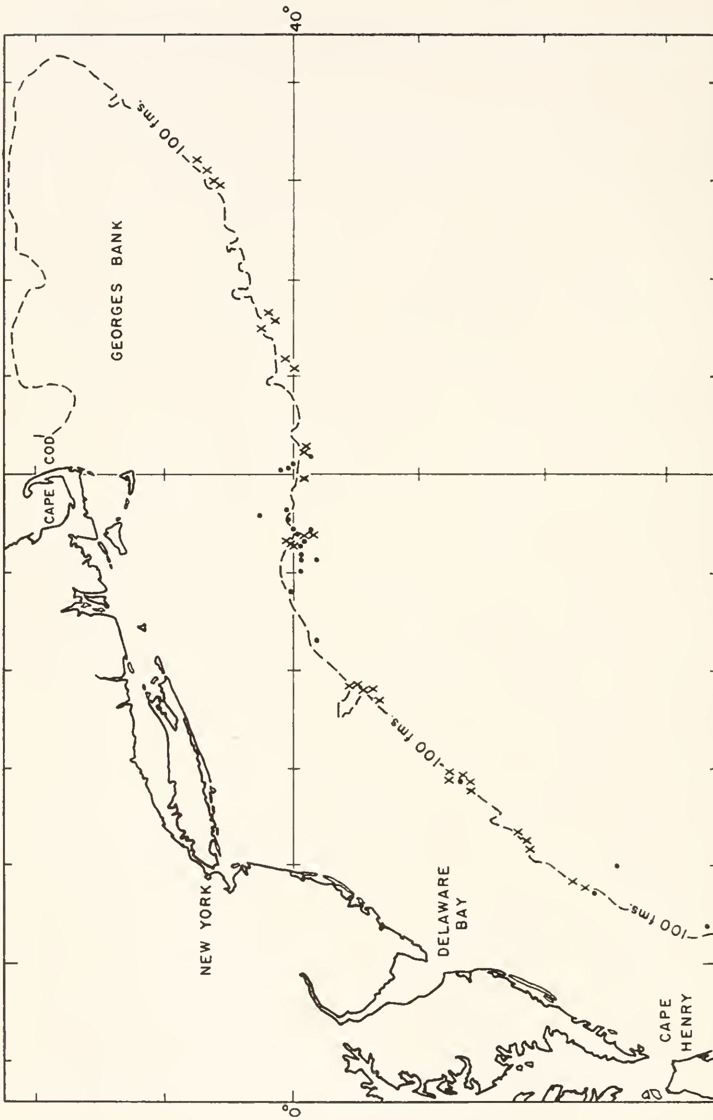

Fig. 2. Localities (●) whence *Merluccius albidus* is represented in the U. S. National Museum from north of Cape Hatteras (information contributed by Dr. Isaac Ginsburg), and (**x**) where it was taken by ''Cap'n Bill II'' in 1953.

one side of the Atlantic, and of *M. merluccius* in the other would still be separated by a gap somewhere near 1400 miles wide, for old reports of the genus off southwestern Greenland are not reliable (Täning, 1938, footnote).

The "Cap'n Bill II" captures, and the earlier locality records as well, were scattered along the outer part of the continental shelf and upper part of the continental slope. Along this zone *albidus* intermingles with the offshore fringe of the population of *M. bilinearis* — the two were taken side by side repeatedly by "Cap'n Bill II" — and it greatly outnumbered *bilinearis* there at the time of the "Cap'n Bill II" cruises as appears from the relative numbers of the two species that were taken (p. 206). It was also more generally distributed than *bilinearis,* to judge from the capture of *albidus* in 47 hauls in 1953 and 1954, but of *bilinearis* in 32 hauls only.

Ginsburg (1954, p. 193) has reported *M. albidus* off Long Island, New York from 58-67 fathoms, also from 317 fathoms (depth of capture of the specimen selected by him as neotype of the species), and the National Museum series includes a record on the southwestern slope of Georges Bank (Lat. 40°01′N, Long. 68°56′W) from as deep as 640 fathoms (information contributed by letter from Dr. Ginsburg). The shoalest "Cap'n Bill II" haul that yielded it was at 50-55 fathoms (shoalest haul made, off Delaware Bay), the deepest was at 545-600 fathoms, the relationship between numbers taken and depth being as follows:

TABLE III

Numbers of *M. albidus* taken at different depths in 1953

Depth in fathoms	No. hauls with *albidus*	Total specimens	Specimens per haul	Average number per haul
50-100	5	27	1–16	5.4
101-200	14	1165	2–220	83.3
201-300[1]	10	1034	48–270	103.4
301-400	6	178	1–84	29.7
401-500	1	1	1	1
501-600	1	22	22	22

[1] One haul working between 250 and 340 fathoms yielded 58 specimens.

Table IV

Generality of distribution of *M. albidus*, versus depth, west of Longitude 66°40′W

Depth in fathoms	No. hauls with *albidus*	Total no. hauls	% with *albidus*
50-100	5	14	35.7
101-200	14	14	100.
201-300	10	10	100.
301-400	6	8	75.
401-500	1	6	16.7
501-600	1	6	16.7

The hauls that took it were all made during the daytime. Hence, from analogy, it seems safe to assume that most of the specimens (if not all of them) were on the bottom when picked up, or very close to it, for European experience is that its close relative *M. merluccius* keeps to the bottom by day, to rise in the water by night in pursuit of the mid-water fishes and squids on which they feed (Hickling, 1927, pp. 78-79; Täning, 1938).

Evidently the center of population for *M. albidus* lies between the 100 fathom and the 300 fathom depth zone. And the "Cap'n Bill II" catches suggest some concentration at about 150-225 fathoms, for the 3 hauls that yielded more than 200 specimens each were at 150 fathoms, at 150-155 fathoms, and at 225 fathoms. This parallels the vertical distribution of *M. merluccius* in north European seas, where it is reported as most frequent between 55 and 275 fathoms (100-500 meters, Belloc, 1929, p. 178), most of the stock wintering deeper than 100 fathoms, but many of them making incursions into water as shoal as 40-60 fathoms in summer (Hickling, 1927), the adults in connection with spawning, the young in pursuit of the smaller fishes on which they prey. The "Cap'n Bill II" catch of 22 *albidus* in a haul working at 545-600 fathoms, and the earlier capture of the species from 640 fathoms (Fish Hawk Sta. 1124; see above), are a little deeper than the greatest depth to which *M. merluccius* has been reported definitely in the eastern side of the Atlantic — 440-550 fathoms (800-1000 meters) according to Belloc (1929, p. 178).

It is interesting, in passing, that while the closely allied *M. bilinearis* comes so close inshore that great numbers are taken in pound nets, the center of abundance for the offshore fringe of the population of *bilinearis* was at about the same depth as for *M. albidus*, i.e. at 100-300 fathoms, as illustrated by Table V.

TABLE V

Numbers of *M. bilinearis* taken at different depths in 1953

Depth in fathoms	No. hauls with *bilinearis*	Total specimens	Specimens per haul	Average no. per haul
50-100	10	47	1-15	4.7
101-200	7	250	1-88	35.7
201-300	6	235	1-100	39.2
301-400	0	0	0	0
401-500	1	3		3

The eight stations where *albidus* was taken shoaler than 100 fathoms in 1953 and 1954 were off Delaware Bay (1 specimen, 50-55 fathoms; 16 specimens, 95-100 fathoms); off Long Island, New York (5 specimens, 81-83 fathoms); off Martha's Vineyard (1, 1, 1 and 2 specimens at 80-93 fathoms, 75 fathoms, 70-72 fathoms and 70 fathoms respectively) and on the southwestern slope of Georges Bank (4 specimens, 85-92 fathoms); 2 specimens were also taken at 100-105 fathoms on the southeastern slope of Georges. Thus it seems as likely to come into shoal water off one part of the coast as another.

These records do not locate the upper limit to its vertical range for the shoalest haul that yielded it (50-55 fathoms, 1 specimen) was the shoalest of the series. But we think it unlikely that it comes nearer to the land than the 70-80 fathom line with any frequency, or in any numbers, partly for the reason that the numbers taken per haul at depths down to 100 fathoms were so small, but chiefly because its presence off the Atlantic coast of the United States could hardly have been overlooked until so recently, if it came close inshore there in numbers at all rivaling those of *M. bilinearis*.

Location of the usual inshore boundary for *albidus* as somewhere between the 55 and 75 fathom lines implies at the same

time that strays only are to be expected closer to the coast than perhaps 50-60 miles anywhere, between the offings of Delaware Bay and of Martha's Vineyard, or between about 90 miles and 180 miles out from the nearest land along the seaward slope of Georges Bank, depending on locality.

An interesting question for the future is whether *M. albidus* ever enters the Gulf of Maine along the bottom of the channel between Georges and Browns Banks, to form a part of the plentiful population of silver hakes that we trawled at depths greater than 65 fathoms in the inner parts of the Gulf in the summer of 1936, i.e. before the possibility was foreseen that two species might be in question, not *bilinearis* alone (Bigelow and Schroeder, 1939, p. 308, Table I).

Our only indications as to the offshore boundary to the range of *M. albidus* are that 22 specimens were taken in the haul that was made the farthest out on the slope, at 545-600 fathoms in 1953 and that the "Fish Hawk" took it at 640 fathoms on the southwestern slope of Georges Bank in 1882 (see above). These depths agree so closely with the maximum recorded for *M. merluccius* in the other side of the Atlantic (p. 212), as to make it unlikely that *albidus* ranges much farther seaward, provided that a wholly pelagic mode of life is not more characteristic of *albidus* than of *M. merluccius,* which regularly seeks the bottom in daytime (p. 212). If this be the case, the breadth of the geographic range of *albidus* is only some 10 to 15 miles at most, anywhere between the offing of Virginia, and the southeastern slope of Georges Bank. And even if it does occur within the Gulf of Maine, the contrast is striking between the breadth of the belt populated by *albidus* in the western side of the Atlantic, and of *M. merluccius* in the eastern, where the range of this hake extends from the mouth of the Baltic to southwestern Iceland in the north, and from the eastern part of the Mediterranean to the continental slope off Gibraltar in the south.

If the range of *albidus* is no more extensive in reality than suggested above, it seems a safe assumption that its total population is much smaller than that of the eastern Atlantic *M. merluccius,* the total catch of which for 1947 (most recent year of record) was about 409,163,270 pounds (185,187 thousands of kilos, see Rosén, 1951, p. 16), shared among Norway, Sweden,

Germany, Denmark, Holland, Belgium, Scotland, England, Ireland, France, Portugal and Spain. This was about 81 per cent as great as the north European catch of haddock, and about 5 times as great as the catch of *M. bilinearis* landed along the middle and north Atlantic coasts of the United States in that same year.

The temperatures at which *M. albidus* was taken in 1953 ranged from 53° down to 38-39°, with the great majority of the catch made at 40.5-52°, as follows:

TABLE VI

Bottom temperatures at stations where *M. albidus* was taken in 1953

Depth in fathoms	Temperature
70-110	53°-49.3°
110-200	52°-42.4°
205-300	42°-39.2°
300-400	40.5°-39°
420-600	39°-38°

A final point of interest is that the distributional status of *albidus* proved about the same for the summer of 1953 as it had been in the 1880's (Fig. 2).

BLUE WHITING

GADUS (subgen. MICROMESISTIUS) POUTASSOU (Risso) 1826

Goode and Bean, writing in 1895 (1895, p. 355), thought it probable that this wide ranging eastern Atlantic member of the cod tribe would "yet be found among the captures of the cod schooners of the offshore banks" off New England. And their forecast has been verified at last, for "Cap'n Bill II" trawled one specimen, about 355 mm. in standard length, on the seaward slope of Georges Bank, Lat. 40°18′N, Long. 68°01′W, at 230-250 fathoms, July 15, 1952, and three others, 349 mm. to 416 mm. long, at 240-280 fathoms on the slope of Browns Bank, between Lat. 42°09′N, Long. 65°21′W, and Lat. 42°08′N, Long. 65°27′W, July 16,

TABLE VII. Blue Whiting of Western and Eastern Atlantic

Specimen no.		1	2	3	4	5	6	7	8
Total length	mm.	349	380	387	416	243	289	291	427
Standard length	mm.	322	347	357	388	224	271	270	401
Eye, horizontal	Percent of head	27.3	24.4	26.1	24.2	28.4	29.4	26.6	24.0
Body, depth	Percent S.L.	13.7	16.8	18.2	16.7	14.7	15.5	14.1	15.5
Head	Percent S.L.	23.9	23.8	24.4	23.9	26.8	25.1	25.7	25.0
Snout to 1st dorsal	Percent S.L.	33.5	36.3	35.9	35.3	37.1	36.5	35.9	37.3
1st, 2nd dorsals, interspace	Percent S.L.	6.8	7.6	7.1	6.4	5.4	6.3	6.5	8.2
2nd, 3rd dorsals, interspace	Percent S.L.	12.4	15.1	14.7	14.3	13.8	11.4	14.8	12.8
1st, 2nd anals, interspace	Percent S.L.	2.2	2.9	1.4	2.6	2.7	1.5	1.9	2.3
Pectoral, length	Percent S.L.	14.9	14.8	15.0	15.2	15.6	14.7	13.7	12.2
Pelvic, length	Percent S.L.	7.5	6.5	8.5	6.4	8.0	6.3	6.7	5.6
1st dorsal, rays	Number	11	11	12	13	12	13	12	12
2nd dorsal, rays	Number	11	12	11	13	11	13	14	12
3rd dorsal, rays	Number	24	23	24	24	22	23	25	24
1st anal, rays	Number	37	33	36	35	36	39	36	34
2nd anal, rays	Number	26	25	25	25	22	23	23	26
Scales	Number	166	181	180	174	170	166	163	167
Gill rakers	Number	5+25	5+24	5+23	5+24	5+23	5+22	5+23	5+23
Pectoral, rays	Number	20	21	21	22	19	21	20	18
Pelvic, rays	Number	6	6	6	6	6	6	6	6
Pyloric caeca	Number	11	9	9	8	a)	a)	a)	10

Specimens Nos. 1 and 4 are from Lat. 42°09'N, Long. 65°21'W, 240-280 fathoms, July 16, 1953; specimen 2 is from Lat. 40°18'N, Long. 68°01'W, 230-250 fathoms, July 15, 1952; specimen 3 is from Lat 42°08'N, Long. 65°27'W, 250-280 fathoms, July 16, 1953; specimen 5 is from off Nice, France; specimens 6 and 8 are from Bergen, Norway; specimen 7 is from Christiania, Norway, these latter four all taken many years ago.

a) The viscera were in such condition that the pyloric caeca either could not be recognized or counted with accuracy.

1953. These have been compared with a *poutassou* about 224 mm. in standard length in the Museum of Comparative Zoology from Nice, France, and 3 others 270 to 401 mm. long, from Bergen and Christiania, Norway, in the U. S. National Museum, loaned to us through the kindness of Dr. Leonard Schultz. The illustration (Fig. 3) and the preceding table (VII) are added so that the reader may judge, first-hand, as to the correctness of our identification:

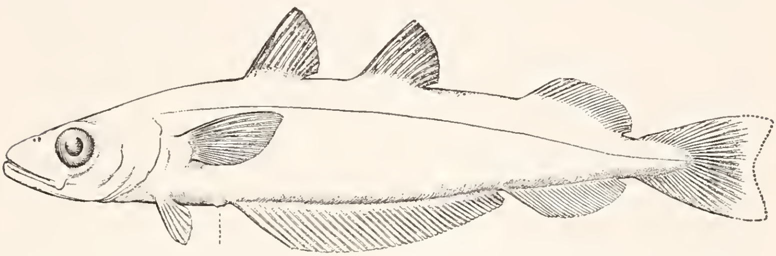

Fig. 3. *Gadus* (*Micromesistius*) *poutassou*, 387 mm. long, from Lat. 42°08′N, Long. 65° 27′W, taken in 250-280 fathoms.

It has been known for many years that the range of *poutassou* in the eastern Atlantic extends from the Mediterranean to Iceland and northern Norway, and from the coastline out across the continental slope. Schmidt (1909, pp. 83-84) has pointed out, also, that the localities where its early stages were taken during the cruises of the "Thor" locate its spawning grounds as near the 550 fathom line, or even deeper still. And since it has been reported recently from the Julianehaab district, West Greenland (Jensen, 1948, p. 182) the "Cap'n Bill II" captures of it off Georges and Browns Bank are not astonishing.

The number of specimens reported so far from the western side of the Atlantic has not been large enough to show whether we are dealing with stragglers, only, as seems true of the European ling (*Molva molva*) recently reported by Templeman and Fleming (1954, p. 11) from the southwestern part of the Grand Bank of Newfoundland, or whether a permanent population exists in the western side of the Atlantic. We are inclined to favor the second alternative, for it does not seem likely that the number of strays crossing the Atlantic would be large enough

for "Cap'n Bill II" to have picked some of them up in two successive summers.

If so, Smitt's (1892, p. 465) account of *poutassou* as without pyloric caeca, would suggest an important anatomical difference between the two populations for there are 8 to 11 of these structures in the "Cap'n Bill II" specimens. But we have recently been informed by Denys W. Tucker of the British Museum (Natural History) that four specimens 241-274 mm. in standard length from Lousy Bank, Lat. 60°20′N, Long. 12°40′ W, 108-200 fathoms, which he examined, had 9, 10, 11 and 12 pyloric caeca, respectively, while one of the Norwegian specimens, mentioned above, has 10 caeca. Thus Smitt's account was incorrect in this respect.

If the blue whiting is in fact a permanent resident of the northwestern Atlantic, the inshore boundary to its regular range probably lies outside the 100 fathom line there, for a fish so easily recognizable could hardly have been overlooked in waters as hard fished as those fronting Nova Scotia and northern New England, if it came close inshore there in such numbers as in the Mediterranean (Risso 1826, p. 228, as *Merlangus vernalis*), in British seas (Day 1880-1884, p. 293), and along the coast of Norway (Smitt 1892, p. 514).

A summary of the nomenclatural history of this species seems appropriate here, to justify our use of the subgenus *Micromesistius* Gill 1863 for it, rather than of any of the other generic or subgeneric names under which it has appeared in scientific literature. The earliest account of it was by Risso (1810, p. 115), as *Gadus merlangus* Linnaeus, 1758. This specific name, however, actually was that of the common whiting of northern Europe, a very different fish, as Risso evidently realized, for he added to his excellent account of it that "ce poisson me paroît une nouvelle espèce" (Risso, 1810, p. 116). Accordingly, he not only proposed the new specific name *poutassou* for it in his next mention of it (Risso, 1826, p. 227), but transferred it from *Gadus* to *Merlangus,* Oken, 1817, a subdivision that had been proposed by Cuvier (1817, p. 213) for such of the gadids as agree with the cod and the haddock in the number of dorsal and anal fins but differ from them in lacking a barbel on the chin.

[1] *Merlangus* was proposed by Oken (1817, p. not numbered, but following p. 1182; the latter misprinted "1782") as the latinized form of Cuvier's (1817, p. 213) "les merlans." See, on this, Jordan, 1917, pp. 97, 100.

This generic allocation for the species *poutassou* was accepted by several subsequent authors; by Moreau (1881, p. 245) for example, and by Jensen (1948) recently. But it has long been realized that *poutassou* differs from the members of the genus *Gadus* as typified by the cod, not only in lacking a chin barbel, but also in a lower jaw projecting beyond the upper, in a vent situated much farther forward with body cavity correspondingly shorter, in a much longer 1st anal fin, in a lateral line that is almost straight, and in having only 1-3 teeth on either side of the front of the vomer (Smitt, 1892, p. 512).

Views have differed as to which of these characters are the more significant, from the taxonomic standpoint. Thus Bonaparte (1846) referred *poutassou* to the genus *Pollachius* Nilsson 1846[1] because of its projecting lower jaw. But Günther (1862, p. 338), followed by Malm (1877, p. 486) and by several subsequent authors, placed it in *Boreogadus* Günther 1862, proposed by Günther (1862, p. 327) as a "group" of *Gadus*, distinct from *Pollachius* (which he treated also as a "group") because with "teeth in the outer series of the upper jaw stronger than the others." The next landmark in the history of the species was Gill's 1863 (p. 231) proposal of a new genus *Micromesistius* for it, which Gill set off from *Pollachius* Nilsson 1846 by "dentition, the very short abdomen, very long first anal and short second dorsal which is widely separated from the first and third."[2] *Micromesistius* was accepted by Goode and Bean (1895, p. 355). Most, if not all, of the references that were made to the species *poutassou* for the next 40 years were either under *Gadus*, as by Smitt (1892, p. 511), Schmidt (1905, p. 58; 1906, p. 11), Damas (1909, p. 210), Williamson (1909), Hickling (1927, p. 79), D'Ancona (1931), Koefoed (1927, p. 118), Nobre (1935, p. 169) and Lübbert and Ehrenbaum (1936, p. 117), or under *Boreogadus* as a subgenus of *Gadus*, as by Day (1880-1884, Vol. 1, p. 275), by Holt and Calderwood (1895, p. 430) and by Cligny (1905). But Norman (1937, p. 51) revived *Micromesistius* for his new species *australis* from southern Argentina,

[1] Nilsson gave no definition for his genus *Pollachius*. But Bonaparte (1846, p. 45) listed *Gadus pollachius* Linnaeus 1758 as its type. And subsequent authors have followed Bonaparte in this regard.

[2] Two pages farther along in the same publication Gill (1863, p. 233) proposed a second new genus *Brachymesistius* for *poutassou*, apparently having forgotten that he had already proposed *Micromesistius* for it.

and this revival of the genus has been accepted by Svetovidov (1948) also, to include both *australis* and *poutassou*.

This disagreement as to the generic status of the species *poutassou* expresses the divergence of opinion now current as to whether it is preferable to emphasize the points of difference among the various gadids that have three separate dorsal fins and two separate anals (Subfamily Gadinae), or the points of resemblance. At the one extreme, Svetovidov (1948) has distributed the 21 full species that he recognizes in the Gadinae among 12 genera, restricting the old genus *Gadus* to the cod (*G. morrhua* Linnaeus 1758) alone, but split into 7 subspecies. And Jensen (1948, p. 140) has recently proposed still another genus (*Phocaegadus*) and a new species (*megalops*) for a West Greenland gadid that had been erroneously reported earlier by Johansen (1912, p. 666) as *G. saida* Lepechin 1773. Similarly, North American ichthyologists as a group have distributed the four common Gadinae of the northeastern United States and of the maritime provinces of Canada, cod, tomcod, haddock, and American pollock among as many genera, *Gadus* Linnaeus 1758, *Microgadus* Gill 1865, *Melanogrammus* Gill 1862, and *Pollachius* Nilsson 1846. And Jordan and Evermann (1898) not only retained the genus *Eleginus* Fischer 1813 for *navaga*, with *Boreogadus* Günther 1862 for *saida*, but recognized a separate genus, *Therargra* Lucas 1898 for the so-called Alaska pollock or Alaska whiting, *chalcogramma* Pallas 1814, in their survey of the Gadidae of North America.

On the other hand, Day (1880-1884), Smitt (1892), Williamson (1909) and Damas (1909), as well as European fisheries biologists in general have interpreted the old genus *Gadus*, or one or other subgenus of the latter, widely enough to include all the Gadinae of northern European and Greenland waters, except for *argenteus* Guichenot 1850, with its close ally *thori* Schmidt 1914, which have commonly been referred to the genus *Gadiculus* Guichenot 1850.

One reason for this divergence of opinion is that students have disagreed as to how much weight should be accorded in taxonomy to skeletal characters in this particular group of bony fishes; a second reason is that all of the external characters that have been proposed as generic in this case are intergrading in

nature. Thus an unbroken series of intermediates connects the projecting upper jaw of cod and haddock with the projecting lower jaw of European pollack (*pollachius*), American pollock (*virens*), and Alaskan pollock (*chalcogrammus*). Similarly, while the contrast in the relative lengths of the two anal fins is sharp between *poutassou*, in which the first is about 2⅓ times as long as the second, and *saida* in which it is only a little the longer of the two, the gap is bridged by *minutus* and by *merlangus* in which the first anal is about twice as long as the second, and by the cod, by the European whiting (*merlangus*), and by *esmarki* in which it is only 1.3-1.5 times as long as the second.

Corresponding to this variation in the relative lengths of the two anal fins, the position of the vent ranges from below the point of origin of the first dorsal fin or a little anterior to the latter, as in *poutassou* and in *luscus*, to about under the mid-length of the first dorsal as in *merlangus* and below the point of origin of the second dorsal fin, or a little farther rearward still, as in cod, haddock, and several others. Similarly, the rather deeply forked tail fin of *saida* is connected, in form, with the rounded caudal of the tomcod of eastern North America (*tomcod* Walbaum, 1792) by a series of intermediates among fishes as well known as the American pollock (*virens*), European pollack (*pollachius*), European whiting (*merlangus*), and European bib (*luscus*).

The lateral line, the dark color of which was the basis on which Gill (1862, p. 280) originally instituted the genus *Melanogrammus* for the haddock, ranges from black in the latter, through somewhat darker than the sides as in the European whiting (*merlangus*), about the same hue as the sides in *poutassou*, and slightly but definitely paler than the sides in American pollock (*virens*) to conspicuously paler than the sides as in the cod. Again, the gap between the various Gadinae with well developed chin barbel, such as cod and haddock, and those which have none, such as *merlangus*, *pollachius* and *poutassou*, is bridged by *virens*, where young specimens usually have a small barbel, but the adults do not. Finally, the number of vomerine teeth in *poutassou* (1-3 on each side of the anterior end of the vomer) links the state in the cod, with a cardiform group of about 30 on each side, to the state in *argenteus* with only about

2 flat and seemingly deciduous vomerines on either side on some specimens, but perhaps none at all on others.

Obviously, the various European students of late years who have been content to leave the haddock in the same genus as the cod, despite its heavier, denser clavicular bones, have not given this character as much weight as their American colleagues who place the haddock in the separate monotypic genus *Melanogrammus*. And while the hyomandibular bone of *poutassou*, and of its close ally *australis* of southern Argentina, is more simple in outline than in most of the other Gadinae as pictured by Svetovidov (1948, pls. 41-64), we think it unlikely that its nature would be accepted any more generally as a generic character for *poutassou* than the nature of the clavicular bones has been for the haddock. In short we face, in the *poutassou*, one of those situations where a species, or group of species, is set apart from the type of the genus nearest to which it falls by a combination of characters that give it a strikingly different aspect, though no one of these characters is strictly alternative. Under these circumstances we think the course the most likely to stand is to retain *Micromesistius* for it, but as a subgenus of *Gadus* rather than as a separate genus.

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NOTES ON SEVERAL SPECIES OF THE EARTHWORM GENUS *DIPLOCARDIA* GARMAN 1888

By

G. E. Gates

With One Plate

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

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No. 3—*Notes on Several Species of the Earthworm Genus* DIPLOCARDIA *Garman 1888*

By G. E. Gates

The material on which this contribution is based comprises miscellaneous lots recently received for identification. All of them are of special interest as little is known about any of these native earthworms of a genus restricted to United States and Mexico.

The author's thanks are extended to the following: Dr. C. W. F. Muesebeck, for making arrangements for obtaining intercepted specimens. Dr. Elisabeth Deichmann, for measurements of penial setae. Dr. Fenner Chace Jr., for various courtesies and for securing the additional material from Oklahoma. Mr. Ottys Sanders who has been on the lookout for sexual individuals of the large Texan species during the last 25 years, for information and material. Dr. G. E. Pickford, for material and for oligochaete separates from the estate of the late Dr. L. Cernosvitov. This latter gift has been especially valued as the author's library was destroyed during World War II.

Diplocardia alba Gates 1943

Subspecies *mexicana* subsp. n. (?)

In soil with chrysanthemum plant from Mexico arriving at Gateway Bridge, Brownsville, Texas, 2/20/50, 1 clitellate specimen in three pieces. (A posterior fragment in the same tube presumably is of the same species.)

External characteristics. Length, *ca.* 60 mm. Diameter, *ca.* 3 mm. Segments, *ca.* 136. Prostomium slightly proepilobous. Clitellum slightly tumescent, dark brownish, annular, extending from 12/13 to 18/19 but lacking ventrally on xviii.

Spermathecal pores in *AB*, slightly nearer equators than intersegmental furrows, on viii/aq and ix/pq. A ventral tumescence reaches laterally on each side to *C* on viii and ix.

Seminal grooves nearly straight, in *AB*, each on a longitudinally placed, parietal tumescence that extends from *A* to m*BC*. A deep transverse furrow, apparently slightly postsetal (19/20 unrecognizable in *BB*), ends on each side at *C* on xix.

Internal anatomy. Septum 5/6 membranous, 6/7-11/12 mus-

cular. Oesophagus with several low but rather thick longitudinal ridges on inner wall in xii-xiv. Intestinal origin in xvii. Typhlosole small, lamelliform, beginning in xx.

Prostates flattened, each in a U-shape. Prostatic ducts slender, almost straight, passing into parietes about at *B*. A penisetal follicle is slightly protuberant into the coelom near *A* in xviii and xx.

Spermathecal duct longer than the ampulla, an ental portion rather barrel-shaped, gradually narrowing ectally and quite slender in the parietes. Diverticulum flattened, vertical, ventrally directed, on anterior (?) face of ental part of duct.

Follicles of *a* and *b* setae of viii and ix are enlarged and slightly protuberant into coelomic cavity.

Life history. Male funnels and seminal chambers of spermathecal diverticula are iridescent. Reproduction obviously is sexual (biparental). The breeding season just as obviously includes February.

Remarks. The anatomy, unless otherwise indicated above, is as in *alba* except for location of the first dorsal pore (not determinable) and the copulatory and penial setae (not examined).

D. alba is known only from a series of 49 specimens collected at Fort Myers, Florida. Spermathecal pores, according to that sample are migrating posteriorly from the primitive location on intersegmental furrows 7/8 and 8/9. The posterior pores have moved further than the other pair but had only just reached the equator of ix in one worm. Posterior pores already are definitely postequatorial in the Mexican specimen but the intestinal origin still is in xvii (rather than xviii, Fort Myers). The only other difference recognized is extension of the clitellum over xviii in the Mexican subspecies.

For each of the two detected cases (cf. p. 236) of accidental transportation of diplocardias there must have been very many others, some even to foreign lands. Successful colonizations (after accidental introductions) apparently are not to be expected outside of the United States and Mexico but cannot yet be ruled out within the generic range.

Diplocardia communis Garman 1888

Chapel Hill, North Carolina, April 19, 1932, 2 clitellate specimens. J. M. Valentine per Dr. G. E. Pickford.

External characteristics. Length, 120 mm. Diameter (through clitellum), 6 mm. Segments, 149, 191. Unpigmented (formalin preservation). Prostomium epilobous, *ca.* ½, tongue possibly closed (? peristomium deeply grooved all around). Secondary annulations; one postsetal secondary furrow per segment from iv back and one presetal from v or vi, posteriorly tertiary furrows may be present but often incomplete. Setae begin on ii; AB *ca.*=or a trifle $< CD$, $BC < AA$, DD *ca.*=½C. First dorsal pore on 8/9 (1), 9/10 (1). Clitellum markedly tumescent, dark red, saddle-shaped, reaching ventrally nearly to A or B, on xii-xix but not as thick on the first and last segments. Epidermis thickened and red on the presetal portion of xiv in AA.

Spermathecal pores on vii-ix, slightly behind intersegmental furrows, on or just lateral to A, at tips of slight tumescences projecting anteriorly in a somewhat pointed and conical fashion over the intersegmental furrows. Female pores probably anteromedian to a and nearer to that seta than to each other. No specially demarcated male field. Seminal grooves between equators of xviii and xx, slightly concave laterally, deep and wide, margins quite tumescent and especially at the ends. Male pores not recognized but possibly on very small white tubercles in the seminal grooves just behind 18/19.

Genital markings paired, transversely elliptical, reaching slightly beyond both A and B, possibly primarily postsetal but definitely crossing intersegmental furrows. Each marking has a distinct greyish translucent center which may be differentiated into outer and inner zones, and an opaque, tumescent, marginal band. Locations are as follows: on 10/11-12/13, 17/18, 20/21-21/22 (1), 10/11-11/12, 22/23-24/25 (1).

Internal anatomy. Septum 5/6 membranous, 6/7-10/11 thickly muscular.

Gizzards in v-vi (2). Oesophagus with numerous, low, blood-filled, irregularly zigzagged, longitudinal ridges which may in part be constricted into villiform protuberances on the inner wall in x-xv. Valve in xvi and anterior half of xvii. Intestinal

origin in xvii (2) but inner face of gut from xvii through xx or xxiii has a distinctly different appearance from that of the remaining part of the tube and the coelomic face is whitish. Typhlosole begins in xix or xx and is rather low but lamelliform to *ca.* lxx from whence posteriorly it is represented only by a flat and strap-shaped thickening at mD that shortly disappears.

Dorsal blood vessel double from vii to the hind end. Behind xxiii disjunct midsegmental portions are in contact and may be rather short. Supra-oesophageal trunk recognizable only in x-xii and anteriorly in xiii. No subneural trunk. Hearts of x-xii apparently latero-oesophageal but the dorsal bifurcations are filamentous. Last hearts in xii (2). Paired preseptal branches from the dorsal vessel present from xiv posteriorly, each vessel long, looped, covered with so much chloragogen as to be quite conspicuous.

Nephridia small but reach laterally to or beyond *D,* avesiculate, ducts slender and gradually narrowed as they pass dorsally, disappearing from sight and possibly into the parietes well above *D.* Each tubule in the clitellar segments is in three distinct clusters of short loops connected only, so far as can be seen, by a delicate filament which is assumed to provide continuity between the clusters.

Brain apparently in ii, posterior margin concave.

Prostates fairly large and extending through part or all of xvii-xxiv. Prostatic duct 3 + mm. long, looped. Vasa deferentia are recognizable from the interior and can be traced lateral to anterior prostatic ducts and into xix where they disappear into the body wall. Penisetal follicles very close together ectally and apparently passing into parietes on anterior faces of prostatic ducts, the *a* and *b* follicles separated from each other only by a delicate strand of tissue. Each follicle contains one functional seta and a very short reserve (tip portion only). Size; *ca.* 1.1 mm. long $\times$ 0.02 mm. thick near base. Shaft very gradually narrowed ectally, only slightly curved or arced. Tip may be flattened slightly on two sides but ectal margin is rounded not truncate. Ornamentation of several circles (complete?) or shorter transverse ridges or rows of small teeth.

Spermathecae may reach up to level of dorsal face of gut, the size decreasing anteriorly. Duct much shorter than the slightly

thicker and usually rather sausage-shaped ampulla, wall rather thick, lumen slit-like in transverse section. Diverticulum sessile on lateral face of duct about midway between ectal and ental ends or even a trifle more ventral, spheroidal, sausage-shaped, or with several marginal incisions. Follicles of ventral setae of vi-x do not project into the coelom. Oviducts not widened, gradually narrowing from 13/14.

Genital markings apparently are areas of epidermal thickening and modification only as no glandular material is recognizable in the muscular layers.

Life history. The clitellum may well have reached maximum tumescence. Brilliant iridescence on male funnels and in spermathecal diverticula shows that sperm had been produced and received in copulation. Reproduction clearly is biparental and a spring breeding season is indicated.

Remarks. The spermathecal pores in *communis*, according to Garman, are "at the anterior edge of" vii-ix, presumably meaning thereby just behind the intersegmental furrows as in the Carolina worms. Spermathecal pores of *Perichaeta* sp. (= *Pheretima diffringens*) were said, in the same contribution (Garman, 1888, p. 74), to be "at the anterior edge" of vi-ix. In this species however the apertures are actually on the intersegmental furrows. It is not therefore certain that the locations in the types of *communis* were intra-segmental. Intersegmental locations are listed for *communis* by Smith (1915), Olson (1928 and 1936) and Causey (1952) but segmental locations were recorded by Eisen (1900). The latter not only had Illinois material that may have been topotypical but did distinguish, in his specific diagnoses, between the two types of locations (cf. p. 242).

The various differences between the Carolina worms and those studied by Garman and Eisen are all small. What importance is to be attached to such differences awaits determination of variation in the type region (locality not precisely stated) and/or elsewhere.

Diplocardia fusca Gates 1943

Dallas, Texas, February 1954, 1 clitellate specimen. Ottys Sanders. (A number of juvenile and aclitellate specimens collected in the same region, in spring, summer and early fall, also have been

supplied by Mr. Sanders at various times from 1930 to date.)
Victoria, Texas, on ground under log in river bottom, Jan. 5, 1915, 1 aclitellate specimen. J. D. Mitchell. (U. S. Nat. Mus. No. 57889.)

External characteristics. Size, 220 x 8 mm. (strongly contracted clitellate worm), to 380 x 8 mm. (other specimens, also strongly contracted). Segments, 311 (clitellate worm). Pigmentation especially dense in the dorsum of xi-xii, rather dense in xxi but elsewhere sparse and unevenly deposited or not certainly distinguishable from alcoholic browning. Setae unrecognizable on preclitellar segments, elsewhere *AB* appears to be smaller than *CD*. The first dorsal pore is on 11/12 (clitellate worm), 10/11 (several others). The clitellum is markedly tumescent, the dorsal pores occluded and intersegmental furrows only faintly indicated (setae?), gradually becoming thinner ventrally and possibly lacking in *AA* on xiii-xvii, lacking ventrally on xviii-xx, bounded anteroposteriorly by 12/13 and 20/21.

Female pores are anteromedian to *a* and nearer those setae than to each other. Male pores were not recognizable, even after tracing the male ducts through the parietes but must be in the seminal grooves and near the equator of xix. Genital markings lacking.

Internal anatomy. Septum 5/6 is muscular. Intestinal origin in xvii (clitellate worm and several others). The typhlosole begins in region of xxiv, is 1½ mm. high, lamelliform, and ends abruptly in ccxxxv (of 311 segments). The dorsal blood vessel is double from vii-xlix, single in vi, double in v, thence anteriorly empty and unrecognizable.

Male funnels, in x-xi, are large, plicate, only slightly iridescent. Seminal vesicles are medium-sized. Prostates are rather small and confined to one or two segments. Penisetal follicles are unrecognizable in xviii and xx though gaps in the longitudinal musculature are obvious, not only on the median side of each prostatic duct (*b*) but also further mesially (*a*). The *a* and *b* follicles of xviii and xx (but not those of xix) were found after removal of the longitudinal musculature. These follicles are a trifle smaller than those of xxi and xvii. Setae are sightly sigmoid though a nodulus is almost unrecognizable. The tip is ornamented with about 15 quite irregular circles of very small

teeth, irregularly and frequently interrupted. No follicles are protuberant from the parietes in the spermathecal region.

The spermathecal duct is slender in the parietes, gradually widened entally, as also its lumen, but there is no definite demarcation of ampulla recognizable either externally or internally. The diverticulum is a vertical row of four or five seminal chambers of varying size, the ectalmost the largest. The diverticular stalk is very short and slender, from proximal face of diverticulum slightly above midpoint. Above the stalk the diverticulum is adherent to the main axis but is free below. The material within the diverticulum has a slight iridescence and is so tough that it can be dissected out intact as a "cast" of the stalk-diverticulum lumen.

Juveniles. The *a* and *b* setae are present in xviii and xx but are lacking in xix.

Life history. Reproduction apparently is sexual (biparental) and possibly in the winter as the only clitellate specimen that has been available hitherto was obtained in February. One other clitellate worm was obtained by Mr. Sanders in the same month (but it died before preservation). Every one of a number of specimens he forwarded at various times from 1930 on, except for the one described above, has been juvenile or aclitellate. These, as noted above, were secured in spring, summer or early fall. Several of the worms supplied by Mr. Sanders probably were postsexual aclitellates but it is now impossible to say more than that as most of the records were destroyed in Burma during World War II.

Habits. Worms of this species, according to Mr. Sanders, cast on the surface of the ground, especially in the spring.

Castings are described by Mr. Sanders (*in lit.*) as follows: "The larger mounds are about 10 cm. in diameter and 2.5 cm. in height. The mound (pl.) does not rise to a sharp apex but a broader one crowned with coarse pellets. Mounds usually are about six inches apart when clustered but may be even closer or several feet away from each other. Castings are distinguishable from those of ants by the size of the pellets. (The size of the earthworm may be judged, to some extent, by the size of the castings.) After pouring a vermicide on the castings worms emerge six inches to farther away from the mound." The cast-

ings sent by Mr. Sanders show that intestinal contents are deposited in piles of long cords *ca* 2 mm. thick (dried) that are slightly constricted at irregular intervals of 3-5 mm. Many small pieces now are discrete but probably were broken off at the constrictions. Shortly after submergence in water the castings had disintegrated and the mud had settled to the bottom.

Habitats. Agricultural soil. Soil (limestone based, blackland soil) of lawns and other grassy spots (Mr. Sanders). Under logs of river bottoms.

Distribution. Fort Worth, Dallas (alt. 512 ft.), Victoria, and possibly in the hills at Palo Pinto some 70 miles east of Dallas. The species, according to Mr. Sanders, "is widely distributed in the Dallas area."

Remarks. The description above, except as otherwise indicated, refers to the clitellate worm which is the only one that has been available in that condition for study.

Spermathecal locations in this species may have resulted from forward displacement of the ancestral pairs that originally opened externally on 7/8-8/9. Alternatively the quadrithecal condition could have been derived from a sexthecal ancestor (possibly less remote) by elimination of the posterior pair of spermathecae.

A large Texan species which may well be *D. fusca* is frequently used as bait in that state by anglers. These worms, according to Dr. C. A. Moyer, are "brittle, stand high temperature, give off a sticky secretion, make good bait for catfish and white perch but are not taken by the blue-gilled sunfish." The sticky secretion, according to Mr. Sanders (*in lit.*) "has quite an odor and is very difficult to wash off one's hands and the earthworm secretes it most profusely."

Diplocardia invecta n. sp.

In soil around geranium plant arriving from Mexico at Hidalgo, Texas, 5/27/54, 3 aclitellate and 6 clitellate specimens.

External characteristics. Length, 55-63 mm. Diameter, 2-3 mm. Segments, 128, 130, 132, 133. Unpigmented, clitellum with a light yellowish or brownish appearance. Secondary annulation indistinct, behind iv or v comprising one presetal and one

postsetal furrow per segment. Prostomium prolobous and demarcated by a posterior furrow (1), slightly epilobous but without a posterior furrow to tanylobous (5). Setae are retracted, probably small, but begin on ii; $AB<CD<BC<AA$, $DD<$ or $ca.=\frac{1}{2}C$. First dorsal pore on 7/8 (5), 8/9 (3), 9/10 (1). Clitellum annular, between 12/13 and 18/19 (4), reaching only part way onto xviii (1), between 13/14 and 17/18 (1), dorsal pores occluded, intersegmental furrows faintly indicated or unrecognizable, setae present.

Quadrithecal, pores at or just lateral to *A* and slightly behind 7/8 and 8/9. Female pores apparently both present (5) and slightly anteromedian to *a*. Prostatic pores equatorial on xviii and xx, about as far lateral to the aperture of the *b* follicle as the latter is from that of the *a* follicle, both apertures more closely paired than on other segments. Ventral setae of xix apparently lacking and no follicle apertures recognizable. Male field not specially demarcated in any way. Seminal furrows indistinct and rather indefinite, in some worms represented only by lines or bands of greyish translucence always concave laterally.

Genital markings paired, centered about at *A* but not reaching mV, transversely elliptical, postsetal; on xiii (8), xvii (8), possibly also on xx (3?). Markings are tumescent except on one worm where they are represented only by a special whitening of the epidermis. There is no distinct demarcation of a central area and marginal rim as in so many oriental species but on two worms a fine, greyish translucent circle enclosing an opaque (rather than translucent area) is recognizable on each tumescence.

Internal anatomy. Septa 6/7-8/9 are somewhat thickened.

Gizzards small, in v-vi (6). Oesophagus highly vascular and widened in ix or x to xii or xiii, with very low longitudinal ridges on the inner wall, valvular through xvi. Intestinal origin in xvii (6), apparently just behind 16/17. The typhlosole is lamelliform but quite low. It begins in xxi (1), xxii (2), xxiii (2), or xxiv (1) and ends in c (1) or civ (1). An apparent slight thickening of a middle or even a posterior portion may be an artifact resulting from a differential effect of the preservative.

The dorsal blood vessel is single throughout (6). The last

hearts are in xii (6). No subneural trunk (6). Nephridia are small, extending laterally on parietes slightly beyond *D*.

Holandric, seminal vesicles rather small, acinous, of a rather grey translucent appearance, in ix and xii (6). Prostates are rather short and small but not juvenile, confined to one or two segments, in the latter case xviii-xix and xx-xxi. The ducts are short and slender.

Spermathecae are small and beneath the gut. The diverticulum is a vertically placed row of three to five seminal chambers, with a very short and slender stalk from narrow proximal side to lateral face of duct, and with connective tissue passing from ventral end to posterior face of septum in front.

Life history. No spermatozoal iridescence was recognized on male funnels or in spermathecae of any of the six dissected worms. Prostates may be fully developed but seminal vesicles and spermathecae apparently are not. Clitellar tumescence could have been maximal only in one worm. Presumably age of reproduction had not yet been attained.

Remarks. Follicles of ventral setae of spermathecal and prostatic segments are unrecognizable in the coelomic cavities. Tips of ventral setae of xvii and xix are visible in the follicle apertures. Actual female pores were not seen, the sites indicated by slight depressions with very slight tumescent margins. Metamerism in region of xvii-xxi of one worm is abnormal.

D. invecta is distinguished from *alba* by the presence of genital markings, the simplex condition of the dorsal blood vessel, and the absence of hearts in xiii. With respect to the last two of these characteristics, *invecta* is less advanced than *alba*. Differences from *udei* are: fewer segments; more anterior location of first dorsal pore; slightly more anterior location of spermathecal pores; presence of genital markings in the clitellum; simplex condition of the dorsal trunk in the posterior portion of the body; absence of copulatory setae in viii-ix (or at least of large follicles protuberant into coelomic cavities) and absence of penisetal follicles in the same cavities. Additional differences may be recognizable when fully mature adults can be studied.

Diplocardia ornata Gates 1943

De Queen, Arkansas, 3 miles to the west, 4/27/52, 2 large juvenile

and 7 clitellate specimens. Five miles to the west, 3/30/52, 2 clitellate specimens. Mr. Ottys Sanders.

External characteristics. Size, 45-60 mm. x 2-3 mm. Segments, 114, 116 (March), 124 (last five regenerated?), 141, 146, 148, 150. Pigmentation unrecognizable, parietes translucent (alcoholic preservation). Prostomium, epilobous, *ca.* ½ or less, tongue open (1), closed (5), pointed, bounding furrows meeting at mD well towards ½. Setae begin on ii; $AB < CD < BC < AA$, *DD ca.*=½C or somewhat smaller (?). Nephropores slightly above *D* on clitellar segments, well dorsal on ii, not certainly recognizable elsewhere. First dorsal pore on 9/10 (2), 10/11 (1), 11/12 (3). Clitellum annular except on xiii and xviii, on xiii-xvii (1), xiii-xviii (7), xiv-xvii (1), possibly not developed to full anteroposterior extent on the two odd worms.

Spermathecal pores very small slits surrounded by annular tumescences, slightly behind intersegmental furrows and at or slightly lateral to *A*, on vii-ix. Female pores slightly anteromedian to *a* to which they are nearer than to each other, within a single transverse area of slight epidermal modification. Seminal grooves concave laterally, broad and deep, in *AB*, between equators of xviii and xx. Male pores presumably on very small conical protuberances in the seminal grooves just behind 18/19.

Genital markings rather indistinct, transversely elliptical, paired, centered about at *A*, on 17/18 (4), 16/17 and 17/18 (1).

Internal anatomy. Septa 5/6-6/7 membranous, funnel-shaped, in contact with the gizzards from which they can easily be pushed back; 7/8 transparent but with a slight sheen indicative of presence of muscular fibres; 8/9-10/11 muscular.

Gizzards large (relatively) and in v-vi (11). Oesophagus without especial local widenings, with some slight ridging of inner wall in x-xi or xii but none recognized in xiii; valvular in xvi (6), relaxed, filled with soil and of about the same diameter as in xiv-xv (3). Intestinal origin in xvii (11). Typhlosole begins in region of xix-xxi and is a rather low but still lamelliform ridge.

Dorsal blood vessel in simplex condition as far back as its character can be determined. Supra-oesophageal and extra-oesophageal trunks present though the former usually is empty, the latter median to the hearts. No subneural. Hearts of x-xii

apparently latero-oesophageal but the connectives to the dorsal trunk very delicate and colorless. Last hearts in xii (11).

Nephridia present from ii posteriorly, funnels of the anterior pair not found. Ducts of the anterior pair passing well dorsally. Nephridia seem to be rather small but reach somewhat beyond *D*. No vesicles recognizable.

Brain in ii, slightly bilobed, anterior margin straight, posterior margin with well marked concavity mesially. Nerve cord without marked muscularity in sheath.

Holandric; seminal vesicles acinous, in ix and xii. Prostates usually not confined to one segment, and may extend as far back as into xxiv; ducts slender, straight, *ca.* 1 mm. long, passing into parietes in the gap at *B*, in xviii and xx. A flat, strap-shaped muscle band is inserted on the parietes, in xviii and xx, lateral to *D*. From it there can be separated off, in favorable conditions, two follicles, one passing into the body wall on the anteromedian aspect of the prostatic duct, the other mesially but still lateral to *A*.

Ovaries conspicuous. Ovisacs lacking (? not found). Oviducts on emerging into xiv much swollen, then narrowed again within the parietes, the widened portion sausage-shaped, resting on the body wall, with the parietal continuation (at maximum development) passing down from the under side.

Spermathecae fairly large, reaching up to level of dorsal face of gut or long enough to do so, often flattened out on the parietes or passing through the neural arch of a septum into the preceding segment. Duct shorter than the ampulla which usually is only slightly thicker and sausage-shaped. Diverticulum vertical, sausage-shaped, leaf-shaped, a flattened disc of three or more round lobes, or of various other shapes, usually with a little connective tissue passing from a ventral portion to posterior face of septum in front. Stalk always short, slender, from an ental part to lateral (?) face of duct near ampulla. Contents of a sausage-shaped diverticulum obviously in a single mass that can be dissected out intact. Margins of other diverticula more or less deeply incised. Follicles of ventral setae of vii-ix usually do not protrude into the coelom. From a follicle of vii that did so, one seta, probably a reserve, was obtained. No ornamentation was recognized. The extreme tip was curved over to one

side more than would be expected in an ordinary sigmoid shaft.

Penial setae average about 1.1 mm. in length and 10μ in diameter at or near the ental end. The shaft is slightly arced, gradually narrowed ectally to 5μ or less. An ectal portion usually is deformed, bent, twisted, or wrinkled but occasionally is almost straight. The tip may be flattened on two opposite sides or not. The ectal end is never truncate but usually rounded and when flattened has an appearance of tapering more to a rather bluntly rounded point. The tip always appears to be complete in spite of deformation and is without a terminal filament which likewise is lacking in the very young reserve setae.

Juveniles. These two worms are of adult size but genital markings are unrecognizable. Seminal grooves are not visible but probably not because of condition. Setae and apertures of ventral follicles of xviii-xx are unrecognizable. Seminal vesicles are small or rudimentary, prostates restricted to xviii and xx, spermathecae only slightly protuberant into coelom. Ovaries are small. Oviducts are slightly thickened in one but not in the other worm. Male funnels quite without iridescence.

Abnormality. The clitellum is of maximal extent and possibly tumescence also on the two March worms (5-mile site) with only 114 and 116 segments. Ovaries are large, oviducts swollen, and spermathecae are of normal size but seminal vesicles and prostates are rudimentary. The prostate glands are about as long as their ducts but even thinner and both are concealed from view beneath the nephridia. No iridescence on male funnels or in the spermathecal diverticula.

Life history. The worm with clitellum restricted to xiv-xvii may not be fully mature. Clitellar tumescence is not especially marked and is lacking in *AA*. Seminal vesicles are rather small, like the prostates which are confined to xviii and xx-xxi. Spermathecal diverticula have no iridescence but small spots are recognizable on the male funnels which are not yet as large as in the other clitellate worms. By full maturity the clitellar tumescence might have extended through *AA* as well as across xiii and xviii.

Male funnels and spermathecal diverticula of the other six clitellate April worms are iridescent, of considerable brilliance in several cases. The clitellum may well have reached maximal

tumescence on three or four specimens. Reproduction presumably is biparental and a spring breeding season is indicated for Arkansas. In Tennessee this species apparently breeds (also?) in the fall (Gates, 1943).

Remarks. These worms, probably contracted, were becoming brittle when studied and already were browned by the alcohol. Soaking in water released the cuticle but left intestinal tissue too gelatinous to trace the typhlosole posteriorly. Nephridia are soft, often more or less broken.

Spermathecal pores of the anterior pair may be even closer to the intersegmental furrow than those of the other two pairs and in one worm seemed to be almost on the furrow.

Nephrostomes also were not found for a number of segments behind i but nephridia from iii on through the clitellar region seem to be less well preserved than in ii.

These worms are referred to *ornata* in spite of differences involving prostomium, clitellum, etc., for geographical as well as morphological reasons. *D. singularis,* according to those who studied topotypical material, has its spermathecal pores on the intersegmental furrows.

Diplocardia riparia Smith 1895

Warner (25 miles southeast of Muskogee), Oklahoma, in Dirty Creek bottoms, April 1954, 7 juvenile, 5 aclitellate, 1 clitellate and 1 postsexual (?) aclitellate specimens. Vera Lee Rounds. (U. S. Nat. Mus.)

Muskogee, Oklahoma, 1 juvenile, 1 early clitellate (?), 2 clitellate and 1 postsexual aclitellate (?) specimens. H. & R. earthworm farm per U. S. Nat. Mus. (These specimens probably were from the same site and same person as the first lot and were collected several weeks earlier.)

External characteristics. Length, 50 (smallest juvenile), 130-145 mm. (clitellate). Diameter, 3 (smallest juvenile), 6-8 mm. (clitellate). Segments, 146 (juvenile), 173, 179, 185(2), 194. Pigmentation brown, fairly dense in dorsum of first 12 or 13 segments, or also through xviii, xix or xx, gradually becoming more sparse posteriorly, apparently lacking in most of the intestinal region, obvious again in the last few segments except in regenerates (unpigmented). Pigment is however recognizable

under the binocular, throughout the intestinal region, in fine equatorial lines widened around apertures of setal follicles when continued ventrally. Secondary annulation is well marked, a postsetal secondary furrow present from iii or iv, a presetal furrow present from v or vi, and from vii posteriorly a tertiary furrow present (on dorsum only or all around) on the pre- and post-setal secondary annulus. Prostomium epilobous, *ca.* ½, tongue closed.

Setae may be so deeply retracted as to be unrecognizable on anterior segments but begin in ii; $AB<CD$ especially anteriorly but difference is slight, $AA=BC$ or slightly unequal, DD *ca.*=½C. Nephropores (usually not certainly recognizable, all specimens strongly contracted), apparently at or near D. First dorsal pore on 11/12 or 12/13. Clitellum annular, but thinner in AA, between 12/13 and 18/19 (3), 19/20 (1), possibly reaching slightly onto xix (1), dorsal pores occluded, intersegmental furrows unrecognizable except ventrally (setae?).

Quadrithecal, pores slightly lateral to A and just behind 7/8 and 8/9. Female pores slightly anteromedian to a and much nearer A than to each other (4). Male and prostatic pores not certainly identified but probably in seminal furrows extending in AB between equators of xviii and xx.

Genital markings represented by raised, transversely elliptical, postsetal, paired areas of epidermal tumescence reaching nearly to mV and well into BC, on xvi-xvii (1), Rxvi, xvii, Rxx, xxi (1), xvii (1), xvii, xx and xxi (2), xvii, xx, xxi and xxii (1), xxi (1), xxi-xxii (1). Ventral setae of the segment usually are included in the marking but no demarcation into rim and central area has been recognizable.

Internal anatomy. Septum 5/6 thin, 6/7-9/10 thickly muscular, 10/11 and the next few septa muscular to slightly muscular.

Gizzards in v-vi (15). Oesophagus highly vascular and widened in xii, xii-xiii or xii-xiv, then gradually narrowing, valvular in posterior part of xvi and anteriorly in xvii. Shortly villiform or small, low ridge-like protuberances (transverse or longitudinal) present on inner wall but no definite calciferous lamellae. Intestinal origin posteriorly in xvii (14) or in xviii (1). The typhlosole which begins in xxii (2) or in region of xxiii-xxvi is lamelliform but certainly quite insignificant, unrecognizable

behind lxxiii (specimen of 185 segments).

The dorsal blood vessel is single throughout (13) or double (2) in some part of its length. Hearts of x-xiii latero-oesophageal, the last pair in xiii (15). Six pairs of vessels join the ventral trunk anterior to 6/7, the first two pairs very close together, the anteriormost passing dorsally along with circumpharyngeal nervous commissures and uniting behind the brain to form the dorsal trunk (3). No subneural.

Holandric, seminal vesicles medium-sized, in ix and xii (4). Prostates are fairly large, 10-20 mm. long, and may extend forward into xiv and back to xxvi though long enough to reach further in either direction. The small slit-like lumen is eccentric ectally but is unrecognizable entally in free-hand sections. Prostatic duct slender, 3-4 mm. long. Penisetal follicles attached to each other entally, divergent ectally, one passing into parietes on median face of prostatic duct, the other more mesially, definitely protuberant (though but shortly) into the coelomic cavities. Each contains one seta (no reserves found). Penial setae are *ca.* 1 mm. long, *ca.* 25µ thick at widest, slightly bowed, tapering ectally to a sharp point. Ornamentation ectally of 15 to 20 quite irregular circles of fine teeth, frequently but irregularly interrupted. No setal follicles especially protuberant from parietes in spermathecal region.

Spermathecal duct longer than the ampulla, bulbous, with a slightly narrowed neck-region entally, gradually narrowed ectally and within the parietes. Lumen gradually widened entally or abruptly widened just below level of diverticular junction. Ampulla heart-shaped to ellipsoidal, slightly wider than thickest part of duct. Diverticulum short, vertical, with a very short and slender stalk from middle of proximal face to lateral face of widened portion of duct, with connective tissue passing directly to posterior face of septum in front. Seminal chambers 3-12 in a vertical row.

Juveniles. The small juvenile (50 x 3 mm.) has all four ventral setae of xix protuberant and in line with the same setae of other segments. Ventral setae of xviii and xx are retracted, follicle apertures approximated but those of the *b* setae displaced more than the others. Ventral setae of xix are still present and in the *A* and *B* ranks in the 100 mm. worm but appear to be

lacking (follicle apertures unrecognizable) on the larger juveniles. Prostates are only about one mm. long in the small juvenile and penisetal follicles are just protuberant beyond the parietes. All worms listed as juvenile have not yet developed seminal grooves.

Life history. Reproduction presumably is sexual, i.e., biparental and may take place, in Oklahoma, in winter and/or early spring. Individuals of this species may survive one breeding season to reproduce again after a period of sexual inactivity. One worm without trace of clitellar tumescence does have a dark brown coloration of the dorsum in xiii-xviii that is lacking both anteriorly and posteriorly. No spermatozoal iridescence was recognized on male funnels or in spermathecal seminal chambers but the seminal vesicles are dark, shrunken, and contain brown bodies (probably aggregates of disintegrated phagocytes and other debris). The mass within each spermathecal ampulla is dark brown peripherally and the contents of seminal chambers in the spermathecal diverticula are also brown. Prostates are yellowish or greyish and with an appearance as of a fine black dust deposited in crevices and irregularities. These conditions have not been seen in juveniles or worms that were becoming sexual and are thought to mark an advanced stage of postsexual regression. This part of the life history apparently has not been subjected to careful study in any species of earthworm. In various species of other genera the adults have been thought to die after the first period of reproduction.

Abnormality. The right seminal vesicle of xii had been herniated almost completely into xi in one worm.

Regeneration. Two unregenerate posterior amputees. Tail regenerates: of *ca.* 35 segments at 84/85, of 12 segments at 141/142, of *ca.* 16 segments (metameric abnormality proximally) at *ca.* 144/145 (metameric abnormalities in the intestinal region), of 12 and 15 segments at 142/143 (one of these regenerates with metameric anomalies proximally), of 14 segments at 174/175. The last 19 metameres of the 146-segment juvenile probably are regenerated. The small juvenile (50 x 3 mm.) has an old tail regenerate at 72/73 and a small, metamerically unsegmented, second regenerate (with terminal anus) at 97/98. Regenerates unpigmented.

Remarks. Setae are unrecognizable in the last few (5-6) segments of worms without amputation and posterior regeneration. Nephropores may however be recognizable.

Doubling of the dorsal blood vessel is limited to vi-xvii (1) or is represented only by midsegmental perforations (1), in xiii-xiv, xvii, xxi, xxiii-xxiv. The occurrence of this condition in but two of the fifteen dissected worms permits a guess that it is due to a mutation partially inhibiting dorsal union of paired embryonic anlage. If so, establishment of such a mutation has been involved in the evolution of various species of *Diplocardia* including the genotype.

This species was but briefly characterized by its author. Some additional information as to material from the same general Illinois locality (Havana) was later provided by Eisen (1900). Subsequently, but without morphological data, *riparia* has been recorded from : Terre Haute (Indiana), Franklin, Delaware and Licking counties (Ohio), Cape Girardeau, Perry and St. Louis counties (Missouri), Lincoln (Nebraska), and three localities in Arkansas.

In Oklahoma, worms of this species appear to be distinguishable (from those in Illinois) possibly by the additional segment covered by the clitellum (xix), by the segmental (postsetal) location of the genital markings, the absence of unpaired and median markings, the intestinal origin in xvii instead of xviii. This latter may be of some importance as one of the evolutionary developments in *Diplocardia* is posterior extension of the oesophagus. The elongation which may involve five or more segments probably takes place, as in other genera, by repeated single steps, a segment at a time. In Illinois where the intestinal origin is in xviii, evolution appears now to have proceeded one step further than in Oklahoma. An intestinal origin in xviii in one of the fifteen dissected Oklahoma worms may be attributable to a mutation for oesophageal extension.

No definite statement as to location of the last pair of hearts in this species has been found in the literature. However, Smith (1915, in a table opposite p. 554) did list hearts in xiii. That location was assumed to be correct in constructing the author's key to species (Gates, 1943), and on the same assumption the Oklahoma worms have been referred to *riparia*. As the character

is of considerable taxonomic importance confirmation from topotypical material, as well as for the specimens recorded from various other states, is desirable.

Diplocardia sandersi n. sp.

Dallas, Texas, 2/2/52, 1 clitellate specimen. Mr. Ottys Sanders.

External characteristics. Size, 135 x 7 mm. (strongly contracted). Segments, *ca.* 173. Secondary annulation; one secondary furrow on iv, two on each segment from v posteriorly. Pigmentation unrecognizable (lacking?, alcoholic preservation). Prostomium slightly epilobous, tongue closed. Setae mostly unrecognizable in the preclitellar region, posteriorly $AB < CD < BC < AA$, DD *ca.*$= \frac{1}{2}$C(?). Nephropores possibly slightly above D on clitellar segments and still more dorsally elsewhere(?). First dorsal pore on 10/11, a pore-like marking also present on 9/10. Clitellum annular, markedly tumescent, on xii/2-xix/2.

Sexthecal, spermathecal pores very small, at or close to A (slightly lateral?), slightly behind intersegmental furrows, on vii-ix. Seminal grooves on xviii-xx, concave laterally, in AB. Genital markings indistinct, paired, in AB, on 17/18 (?) and 20/21 (?).

Internal anatomy. Septum 5/6 with some muscularity, 6/7-10/11 thickly muscular, 11/12-13/14 muscular but decreasingly so posteriorly.

Gizzards in v-vi. Oesophagus considerably widened in xi-xv, deeply constricted at septal insertions and moniliform, with low, irregular and interrupted transverse ridges on inner wall, an uninterrupted longitudinal ridge—perhaps of slightly greater height—at mV. Oesophagus valvular in xvi-xvii. Intestinal origin in xviii. Typhlosole begins in xxiv, lamelliform, *ca.* 1.5 mm. high, behind lxxiii represented only by a low and rather irregular, strap-like thickening of the roof which ends in region of cxvii.

Dorsal trunk single throughout. Hearts of x-xiii apparently latero-oesophageal, those of xi-xiii (but not of x) traceable to ventral trunk. Segmental commissures between dorsal and ventral trunks, in the postclitellar portion of the body, are long

and considerably zig-zag-looped.

Nephridial funnels in *AB*, often within considerable clumps of coelomic corpuscles, not found on the tubules of ii. Nephridia extend well beyond *D*.

The brain is in ii and neither anterior nor posterior margin is incised. Absence of sheen on the nerve cord shows that any sheath is not especially muscular. Ganglionic swellings of the cord are very slight.

Holandric, seminal vesicles in ix and xii. (A testis sac or sacs possibly present ventrally in x.) Prostates in xviii and xx-xxi; ducts 2.5 mm. long, no special muscularity or sheen recognizable, ectal half straight, ental half in two small loops. Penial setae apparently lacking. A single vestigial follicle (?) deep in the musculature, somewhat median to the prostatic duct.

Ovaries and oviducal funnels, two pairs, in xii-xiii.

Spermathecae medium-sized, reaching well up alongside gut. Ampulla sausage-shaped, not much wider and somewhat shorter than the duct. The latter is not stout, somewhat narrowed ectally and especially within the parietes. Diverticulum a flattened and rather leaf-like ridge of seven or so seminal chambers, with a very short and slender stalk from the proximal edge near ental end passing to ental end of duct or slightly below. From a ventral portion of the diverticulum connective tissue passes to the septum in front. Discounting twisting, the diverticulum appears to be on the anterior face of the duct. Copulatory setae apparently lacking, no follicles protuberant from the parietes in vii-x.

Life history. The clitellum appears to be at maximal tumescence. Spermatozoal iridescence was not recognized on male funnels but was visible in the sticky contents of the spermathecal diverticula. The seminal vesicles showed no evidence of post-sexual regression. As the worm was obtained in February, the breeding season may be in the winter.

Remarks. The type had been preserved in a strongly contracted condition, in alcohol, and though not yet browned was becoming brittle when studied. Adherence of cuticle to parietes, even after several days in water, prevented recognition of some reproductive apertures and characteristics of the male field, possibly nephropores also. A deep longitudinal grooving at mV

in the clitellar region prevented recognition of female pores and any markings that may have been present there. Supra-oesophageal, subneural and extra-oesophageal trunks are quite unrecognizable. Nephridia are soft and fragment easily. Supposed ducts (blood vessels?) pass well beyond *D* and are without vesicular enlargement or are only slightly widened just as they pass into the parietes.

D. sandersi appears from its size and presence of hearts in xiii to be close to *D. longa* Moore 1904 (Pulaski County, Georgia) from which it is distinguishable as follows: location of gizzards (in v-vi rather than vi-vii); absence of a thick muscular sheath on the nerve cord; attachment of the spermathecal diverticulum to ental end of duct (rather than ectally); hologyny, and possibly by the absence of penial setae. The hologyny may, of course, be sporadic rather than specific. As *longa* is the only species of *Diplocardia* with the gizzards behind v-vi the difference in location now appears to justify specific status for the two taxa though the other differences may at present seem less important.

Diplocardia singularis (Ude) 1893?

Livingston County, Michigan, southwest woods, Edwin S. George Reserve, 1 juvenile and 1 aclitellate anterior fragment, in poor condition. K. K. Bohnsack.

External characteristics. Sexthecal, spermathecal pores slightly lateral to *A*. Female pores probably in *AA*. Seminal grooves on xviii-xx.

Internal anatomy. Rather high longitudinal lamellae present on inner wall of prevalvular portion of oesophagus. Intestinal origin in xvii. Dorsal blood vessel apparently single. Last hearts in xii.

Holandric, seminal vesicles in ix and xii. Spermathecal duct fairly long, erect in coelomic cavity, with muscular sheen though rather slender; diverticulum digitiform (?), attached to ental end of duct and directed ectally; spermathecal ampulla may be bent over and directed ectally on side of duct opposite diverticulum.

Remarks. This appears to be the first record of a *Diplocardia* from Michigan. Condition does not permit recognition of certain characteristics required for a specific identification. The nearest

sexthecal species geographically is *singularis*. Just how that species should be defined is not yet known though it has been reported from numerous localities in Ohio, Indiana, Illinois, Missouri, Arkansas and Louisiana.

DIPLOCARDIA sp.

Warner (25 miles southeast of Muskogee), Oklahoma, in Dirty Creek bottoms, April 1954, 1 small juvenile. Vera Lee Rounds.

External characteristics. Size, 40 x 1.5 mm. Segments, *ca.* 133. Pigmentation quite unrecognizable throughout (formalin preservation). First dorsal pore on 9/10. Ventral setae of xviii-xx unrecognizable but seminal grooves lacking. Spermathecal pores probably on anterior margins of viii-ix, at or just lateral to *A*.

Internal anatomy. Septum 6/7 is muscular, 7/8-8/9 somewhat thicker. Gizzards in v-vi. No special calciferous lamellae on inner wall of prevalvular portion of oesophagus. Intestinal origin in xvii. Typhlosole begins in xx and is definitely lamelliform though not large. Dorsal blood vessel single throughout. No subneural. Last hearts in xii.

Holandric (?), seminal vesicles recognized only in xii. Penisetal follicles much longer than the prostatic duct, apparently passing separately into parietes median to prostates of xviii and xx. Penial setae 1.1-1.3 mm. long, 10-15μ thick. Tip flattened on two sides, tapering to a very short filament which may be bent or curved to one side. One mature and at least one very short reserve seta in each follicle, two extra reserves in one follicle.

Ovaries are much larger than in the smallest juvenile of *riparia* (from the same batch). Spermathecae, juvenile, pass into parietes at *A*, anteriorly in viii-ix, diverticula unrecognizable.

Remarks. This worm probably would have attained sexual maturity at a much smaller size than does *riparia*. Ventral setae of viii-x may be copulatory. The follicles projected slightly into the coelomic cavities but attempts to remove the setae were unsuccessful.

This form runs down in the author's key (Gates, 1942, p. 92) to *D. udei*. The latter has been known hitherto only from descriptions of the types secured at Raleigh, North Carolina. A

doubtful record from Terre Haute, Indiana, never has been confirmed. The Oklahoma worm apparently is distinguishable by location of the spermathecal pores, absence of gut widening in xv and of high calciferous lamellae therein, simplex condition of the dorsal blood vessel posteriorly, and by the terminal filament of the penial setae. Additional differences may be recognizable at maturity.

Diplocardia udei Eisen 1899

Highlands, North Carolina. In soil under moss by stream on path to Primeval Forest (altitude *ca.* 3,900 ft.), July 24, 1931, 1 clitellate specimen. In pocket of sandy black soil (pH 5.0) under dead leaves by stream in forest on path to Primeval Forest, July 27, 1931, 2 early juvenile, 1 aclitellate and 18 clitellate specimens. Virgin Forest, August 20, 1932, 4 early juvenile, 1 late juvenile, 2 aclitellate and 8 clitellate specimens. J. M. Valentine per Dr. G. E. Pickford.

External characteristics. Length, 90-120 mm. (clitellate specimens, not strongly contracted). Diameter, 3-3½ mm. (through clitellum or gizzard region which is the thickest portion of the body). Segments, 159, 166 (posterior amputee), 177, 178, 179, 180, 181. Secondary annulation fairly distinct, a presetal and a postsetal furrow present from v or vi, a tertiary furrow on the first and last secondary annuli of vii-viii and occasionally on one or more additional segments. Pigmentation unrecognizable and probably lacking (formalin preservation). Prostomium, indeterminable (6), possibly epilobous and with open tongue (3), apparently tanylobous (28) with a longitudinal furrow at mD from 1/2 well out onto prostomium (23), with an additional furrow on each side of the tongue (7), with only two longitudinal furrows on the tongue and neither median (5). Setae begin on ii on which all are present; AB *ca.*= or very slightly $< CD < BC < AA$, DD *ca.*$=\frac{1}{2}C$, not closely paired, ventral setae of viii-ix copulatory, of xviii and xx penial, of xix lacking. Nephropores unrecognizable but possibly on most segments at D, probable sites sometimes indicated by slight tumescences. First dorsal pore on 9/10 (1), 10/11 (28), 11/12 (5), not determinable (3, not certainly recognizable anterior to clitellum). Clitellum dark red, annular except on xviii, usually more or less tumescent but

intersegmental furrows and setae present though dorsal pores are occluded, on xiv-xvii with slight reddening of pq/xiii and aq/xviii (3, of which one certainly and another probably in early sexual stage), on xiii-xviii (24), epidermal thickening gradually decreasing in xviii and usually slight or unrecognizable behind the equator though the red coloration is continued to 18/19.

Spermathecal pores minute, on or slightly lateral to *A*, in front of or on the presetal secondary furrows of viii-ix and at least half way towards the equators. Female pores apparently always paired and anteromedian to *a*, (sites obvious though definite apertures recognizable only on 5 specimens). Male and prostatic pores unrecognizable. A male field is not marked off and the region between the seminal grooves is not depressed. Grooves sinuous, in *AB*, between equators of xviii and xx, the margins of the grooves tumescent.

Genital markings transversely elliptical, with greyish translucent, circular centers, in a longitudinal row of 4-7 immediately lateral to each seminal groove, one to three markings on each of xviii-xx, occasionally crossing intersegmental furrows.

Internal anatomy. Septa 5/6-6/7 membranous (streaks of sheen sometimes visible in 6/7), funnel-shaped and must be peeled back from the gizzards to discover insertions on gut; 7/8 slightly muscular, 8/9-9/10 muscular or 7/8-13/14 slightly muscular to muscular.

Gizzards rather large, in v-vi (36). Oesophagus quite obviously widened in xv (36) and with fairly high, thin, white, lamelliform longitudinal ridges some of which are continued but at lower height into xvi where they are continuous with ridges of the valve or forwards even into x. The portion of the gut in xvi may have the same external appearance as the segment in xv or xvii. The valve is short and extends slightly into xvi and xvii (36). Intestinal origin in xvii (36), gut highly vascularized in xvii, less so in xviii-xix. The typhlosole begins in xix (35) or xx (1) but may project slightly into xviii or xix and is nearly one mm. high, lamelliform, height abruptly decreasing in liv and unrecognizable behind lvi (1) or ending in lx (1) but with a flat ribbon-like thickening still recognizable at mD through several further segments (worm with 177 segments).

Dorsal blood vessel single anteriorly, doubled posteriorly (36)

and in cxxi-clxxvii (1) or in the last 66 segments (2 specimens), 60 (2), 59 (1), 56 (1), 46 (1), 40 (1), 36 (1). The doubled portion is short, midsegmental, often easily recognizable because of presence of a bit of chlorogogen in the perforation. The perforation may be lacking (no doubling?) in any particular segment, in two, three or even several consecutive metameres. A quite obvious perforation is present in xlvi of a worm in which doubling was otherwise lacking except in the last 56 segments. Supra-oesophageal trunk adherent to the gut and recognizable only in ix-xii, usually empty. Extra-oesophageals recognizable only in v-vii where they are distended with blood. Subneural trunk lacking (36). A latero-oesophageal vessel in *BC* is recognizable only in ix-xx and may also be doubled. Into these vessels in xiv-xx the segmental branches from the dorsal trunk (long, looped and with chlorogogen) apparently pass. Hearts of x-xii apparently latero-oesophageal but both dorsal bifurcations are filamentous and without blood. Hearts of ix lateral. Last hearts in xii (36 specimens).

Nephridia are present from ii posteriorly and are small, behind the clitellum reaching slightly lateral to *D*, apparently avesiculate. The ducts (?) pass into the parietes at or near *D*.

The brain apparently is in iii, near level of intersegmental furrow 3/4 (17) but septa are unrecognizable dorsally. The posterior margin is very slightly concave. The nerve cord is without marked muscularity of the sheath.

Holandric, seminal vesicles in ix and xii (33, unrecognizable in 3 juveniles), acinous. Vasa deferentia of a side come into contact in xiii or behind 13/14 but do not unite until just before they pass down into the musculature just behind 18/19, occasionally crossing over each other. Prostates, in xviii or xviii-xix and xx or xx-xxi (once one prostate in xx-xix), small, straight or in one or two u-shaped loops. Ducts slender, white, nearly straight or ental portion with one or two loops, 1-1½ mm. long.

Ovaries fairly large, fan-shaped, with long strings of eggs. Oviducts not enlarged, gradually narrowed from the funnel ectally.

Spermathecae medium-sized, usually long enough to reach up to level of dorsal face of gut. Ampulla rather sausage-shaped to ovoidal but not clearly delimited externally from and only

slightly thicker than the duct. The latter is not stout and is slightly narrowed ectally, especially within the body wall. The diverticulum may be a vertical row of 3-7 rounded lobes on the lateral side of the duct with a short stalk from near the upper end or more flattened, fan-shaped and stalkless but also vertical. Occasionally with more than 7 seminal chambers and rather berry-shaped but still vertical. Diverticulum-duct junction always well above the parietes and in many cases apparently near ental end of duct. Connective tissue from diverticulum to septum in front delicate and usually only a slight filament.

Follicles of the copulatory setae, always present in viii-ix (36), project into the coelomic cavities (but not in x or vii) and are united entally with a muscular strand passing laterally to the parietes. Reserves may be present in the coelomic portions of the follicles. The tip of the setal shaft is shortly claw-shaped. Ornamentation, ental to the claw, is of narrow, open, longitudinally placed excavations each of which usually is continued entally into a small pocket of which the outer wall is very thin. Excavations may be so closely crowded that intervening regions have a meshwork appearance in a strictly surface view. The wall of a pocket at sides of shaft, in appropriate optical section, has an appearance of a large, ectally directed triangular tooth or scale. Reserves are red, functional setae yellowish or greenish.

Follicles of the penial setae reach to or well towards the middle of the prostatic duct and are continuous entally with a muscular strand just in front of the septum and inserted into parietes just lateral to *D*. The *b* follicle passes into the body wall on the anterior face of the prostatic duct in the *b* gap and the other follicle into the *a* gap. Shafts are one mm. long, slender and yellowish, slightly arced or with a more marked curvature ectally. The tip narrows gradually but instead of coming to a point is slightly flattened, widened and with a single concavity in the ectal margin. This very small terminal portion, usually lacking, may have an appearance of two very small rounded lobes. Ornamentation is sparse, of very small spines, few and isolated or in several circles. Reserve setae were not recognized.

A small, low mound of soft material, presumably glandular, is present on the parietes in xviii and xx median to the prostatic duct. No glandular material is however recognizable on or in

the body wall immediately beneath the genital markings.

Juveniles. The *a* and *b* setae in xviii and xx are only slightly approximated in the smaller juveniles, those of xix still in line with the same setae of other segments. Ventral setae of xviii and xx are unrecognizable externally on the larger juveniles though in xix they may still be protuberant and normally located. In one late juvenile only one *b* seta is still visible (in normal location) on xix, apertures of other ventral follicles occluded. In this worm there is on each side a slight, almost straight, longitudinal tumescence between the equators of xviii and xx exactly in *AB* and with a slight groove representing the seminal furrow. Genital markings had not appeared. Penisetal follicles in juveniles may reach well towards or even to ental end of prostates.

Abnormality. No. 1. Spiral metamerism near tail end involving three segments. No. 2. Left spermatheca of viii twice length of others. Only a short ental portion slightly widened like an ampulla. Diverticulum (no iridescence) at normal distance from parietes.

Life history. Coelomic cavities of x-xi are packed full of coagulum in each aclitellate and clitellate worm. The vasa deferentia are iridescent in 26 of the clitellate specimens. Spermathecal diverticula have a marked iridescence in 24 and male funnels of 19 have a similar spermatozoal iridescence. Each spermathecal ampulla is occupied by a hard, pink, translucent mass. Reproduction obviously is sexual (biparental) and ovaries usually appear to be mature. Cocoon deposition in July-August may be expected in the Highlands locality if there is adequate moisture.

Regeneration. None. Only one amputee (posterior).

Remarks. In a four foot square area in which the soil above the rock was only one foot deep there were 45 earthworms (including other species).

The worms apparently had been preserved in a relaxed condition admirably suited for determination of location of first dorsal pore. The pores are wide open and in a posterior portion of the soma the dorsal vessel occasionally is protuberant through the openings. The peristomium is however longitudinally furrowed all around and as a result of this wrinkling (?) little importance can be attached to the tanylobous characterization of the pro-

stomium. Genital markings which might have been more difficult of recognition in strong contraction are quite obvious. Recognition of female, male and prostatic pores was no easier than when worms are contracted.

Highlands material differs from the Raleigh types as follows: fewer segments (to 181 instead of 200-220), tanylobous prostomium (instead of epilobous), location of spermathecal pores on or close to *A* (instead of in front of *b*), paired female pores (instead of 1?), extramural spermathecal diverticulum (hidden in wall and perceptible only in sections), and possibly by absence of copulatory setae in x. Genital markings appear to be different. The types may have been less mature than the Highlands worms and preservation may well have been different. For the present then there is no good contraindication to identification as *udei*.

D. udei is more advanced than *D. gracilis* Gates 1943 with respect to development of calciferous lamellae but less advanced with respect to posterior dislocation of spermathecal pores and posterior extension of the oesophagus. *D. gracilis* is however known only from the holotype from somewhere in Tennessee.

DISCUSSION

The genus *Diplocardia,* restricted to the United States and Mexico, is especially interesting because of the marked variation shown in characteristics often uniform throughout a genus or whole groups of genera. Within this genus the oesophagus has been elongated to various levels, intramural calciferous glands occasionally have been closed off, an intestinal typhlosole has been developed sometimes to a stage of ventral bifurcation, the dorsal blood vessel often has been doubled either in one portion or throughout almost all of the soma, penial and copulatory setae have been developed, the spermathecae have been shifted about variously, and the male terminalia—without modification of the ancient quadriprostatic and three-segment pattern—have been translocated posteriorly one, two or even three metameres. Four seminal vesicles, in ix-x or x-xi, presumably have been eliminated. Intrageneric acquisitions also include: a brown pigment, an extra pair of spermathecae (in vii), and an extra pair of hearts (in xiii). Gizzards apparently have been shifted back one segment in a species in which the nerve cord sheath has be-

come thickly muscularized. Except in the excretory system which still remains to be studied, all of the major anatomical changes that have been made in this genus may have been recognized.

Little however is known about any particular species. The diplocardias must have been common in Texas prior to the introduction of various European and Asiatic exotics. In spite of the competition with much more adaptable species to which the diplocardias have been exposed they may still be fairly common in that state (p. 236). Nevertheless, for the whole of Texas, records have been found of the identification of only three specimens. Larger numbers of identifications have been reported for each of several other states but often (5 states) without descriptions or even any records as to variation. Early descriptions of various species, now inadequate, still have to be corrected and supplemented, preferably from topotypical material in longer series than were originally available or utilized. Nor is there much more certainty now than previously (Gates, 1943) as to just what characteristics, or combinations of them, warrant specific status.

The material of the present as well as of the previous contribution (1943) already has provided instances of individual variation in some of the characteristics by which species have been distinguished and defined. Furthermore, the constant necessity for mention of differences from material previously examined (cf. *ornata* from Tennessee and Oklahoma, *udei* from Raleigh and the mountains of western North Carolina, *communis* from North Carolina and Illinois, etc., on previous pages, and also Eisen, 1900, Heimburger, 1915) is at least suggestive of geographical variation. Further detailed studies can be expected to obviate unnecessary erection of new species and enable suppression of some species or reduction to subspecific status. Thus, for instance, *D. singularis*, *caroliniana* Eisen 1899 and *ornata* seem to be variations on a common theme and other instances of similar sort could be cited.

Doubling of the dorsal blood vessel, as already noted, begins at or close to the anterior end or only towards the anal region. In the former case the doubling may be continued through the clitellar region only (*alba*), somewhat more posteriorly (*fusca*)

or even to the hind end of the body (*communis*). When the duplicity is only posterior there also may be considerable variation in the size of the region involved. Genetic determiners for this major evolutionary change presumably prevent mid-dorsal fusion of paired embryonic anlage except in regions of septal insertions and evidently become operative at various stages of development. In species such as *fusca* these determiners become ineffective rather early in embryonic growth.

The diplocardias, once common in southern Illinois, were thought years ago (cf. Smith, 1928) to be disappearing in competition with the exotics which have been increasingly distributed ever since, both accidentally and deliberately (Gates, 1954), throughout much of this country. If these peregrine forms are as successfully competitive as Smith, and indeed others, thought it may already be too late for conservation of some important races even in museum alcohol. In Texas, and presumably also certain other parts of the generic range, there still seems to be an opportunity to learn much about the evolution of this American genus.

SUMMARY

Material of *D. alba mexicana* n. subsp., *communis* (from North Carolina), *invecta* n. sp. (Mexico), *ornata* (Arkansas), *riparia* (Oklahoma), *sandersi,* n. sp. (Texas), *udei* (mountains of western North Carolina), as well as the first clitellate specimen of the large Texan *fusca,* is described, with data on variation and notes on abnormality, life history, regeneration, habitats and habits. Successful colonization after accidental transportation may have taken place within or near the proper generic range but is not expected elsewhere. Little is known about any species but major intrageneric evolutionary changes in anatomy probably have been recognized and are listed. Considerable geographic variation seems to be indicated by the data now available. Genetic determiners for doubling of the dorsal blood vessel become operative at different stages of development but in some species become ineffective rather early. Although diplocardias long may have been disappearing in areas affected by intensive cultivation or other human activity, less disturbed regions apparently still may provide opportunities for study of a genus restricted to the United States and Mexico.

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PLATE

Photograph of a single mound of castings deposited by *D. fusca.* Courtesy of Mr. and Mrs. Sanders.

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 113, No. 4

A STUDY OF LeCONTE'S SPECIES OF THE CHRYSOMELID GENUS *GRAPHOPS* WITH DESCRIPTIONS OF SOME NEW SPECIES

By Doris H. Blake

With Six Plates

CAMBRIDGE, MASS., U. S. A.

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Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 1, no. 18 is current.

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No. 4—*A Study of LeConte's Species of the Chrysomelid Genus* GRAPHOPS *with Descriptions of some New Species*

By Doris H. Blake

For the last 20 years of his life the late Herbert Spencer Barber was interested among other things in the genus *Graphops*. He left a manuscript that consists of notes on the different species, in particular the strawberry rootworm, *G. marcassita* (Crotch), as well as a description of the genus and key to the species. In the U. S. National Museum collection he had distinguished five new species and attached manuscript names to them. Two of these are old species that he failed to recognize, never having had a chance to examine the LeConte types until a few weeks before his death. It was no fault of his that he did not recognize these species because they are all much alike and the short descriptions by LeConte in his posthumously published key are not sufficient to differentiate them. Mr. Barber's handwritten pages for the most part amount to disconnected notes that he made at intervals during his busy years of identification work. His key I cannot use since he recognized only 9 species whereas I have 18. I have worked with much more material than he had, from collections that have been lent me. Likewise his description of the genus, which is mainly made up of a discussion of the specific differences, is not adequate. I have been more fortunate than he in that I have been able to examine LeConte's types at regular intervals during my study. Moreover I have had time for concentrated work which Mr. Barber never had. Great credit should be given him for the many fine dissections that he made of the specimens that from time to time came into the collection.

The first two species of the Chrysomelid genus *Graphops, pubescens* and *curtipennis,* were described by Melsheimer[1] in 1847 under the genus *Eumolpus*. In 1859 LeConte[2] described *nebulosa* and *smaragdula* under the old Chevrolat generic name *Heteraspis,* unaware that the name had been used by Blanchard[3] for African and East Indian species. Blanchard in starring the

[1] Melsheimer, Proc. Acad. Nat. Sci. Phila., vol. 3, 1847, p. 169.
[2] LeConte, Coleop. Kansas and New Mexico, Smithsonian Contrib., 1859, pp. 23, 24.
[3] Blanchard, Emile, Histoire des Insectes, vol. 2, 1845, pp. 186, 190.

monobasic on *Eumolpus vittatus* Olivier, the formal designation of that species as its genotype was done by Chevrolat 1845 (in D'Orbigny Dict. d'Hist. Nat., vol. 6, p. 596). *Scelodonta* Westwood (monobasic type, *S. curculionoides* Westwood) seems to be a junior synonym of *Heteraspis*." Thus, if the two genera were to be united, the North American species would revert to LeConte's first genus, *Heteraspis*.

LeConte briefly summarized the salient characters of the genus *Graphops* as follows: (1) being pubescent; (2) the head as having two deep impressed lines connected in front between the antennae and running obliquely backwards and curving around the upper and back margin of the eyes; in *Metachroma* the lines are in front of the antenna; (3) the prosternum has a straight outline beneath; and (4) the claws are variable in the extent of the basal tooth.

To this brief description may be added that the head is more or less densely punctate and pubescent, with a median depressed line or simply a median depression above the transverse line connecting the deep cleft about the eyes. This transverse line, in reality made up of two lines forming an angle and usually at the peak uniting with the depressed median line, is variable in the extent to which it is impressed. In a few species there is little evidence of it, and the upper and lower front are not separated by it. But ordinarily there is an impressed line or depression or even sulcus between the upper and lower front. In the lower front the clypeus or region right over the mouth is variously shaped. In some species it is deeply and angularly emarginate, in others feebly angularly emarginate, grading into roundly emarginate, and rarely almost straight or truncate across. The antennae present little difference in the various species, the first joint is large and rounded, the next five small, shiny and subequal, and the distal joints wider and hairier. The antennae do not come much below the humeri. The pronotum varies in shape and the degree of punctation. It is always wider than long, rounded more or less on the sides, without depressions, and more or less punctate and pubescent, often with small smooth roundish areas. The scutellum is usually pentagonal, like that of *Heteraspis,* whence the name "different shield." The elytra are usually wider than the prothorax and

vary in length, from long in *pubescens* to short in *curtipennis.* Compared with the humeri in the Oriental species, the humeri in these are small as well might be the case in beetles with poorly developed wings. The elytral punctation is striate although in a few species there are punctures between the striae that make the elytra seem confusedly punctate. The pubescence is variable, in some the elytra have patches of denser pubescence, in others, the hairs are evenly distributed, or as in *curtipennis,* in lines converging towards the suture at the apex. In one species from Arizona the pubescence is so inconspicuous as to be almost absent, whereas in other species it is so long and heavy as to obscure the punctation below. In all, the pubescence is white. There are some brilliantly metallic species and usually these are larger, but the majority are small, 2 to 5 mm. long, and black or bronzy. There is usually great variation within a species, some specimens may be bronzy and others bright metallic green. The body beneath is more or less coarsely punctate with the legs also punctate, and the pubescence is often dense on the sides of the breast and sides of the abdomen. The femora are robust and the front ones of a few species minutely toothed. The tibiae of the middle and posterior legs are emarginate near the apex, and the claws have a longer or shorter basal tooth. In *G. nebulosa* and related species the claws are more widely separated. In most species the wings are not well developed and in an Arizona species they are so small that it is doubtful whether the beetle can fly at all.

Three species, *G. pubescens* (Mels.), *G. curtipennis* (Mels.) and *G. marcassita* (Crotch) appear to occur in abundance and are found in a wide range from the Atlantic coast westward. The rest of the species are not at all well represented in most collections examined. This may be due to the fact that the beetles are overlooked because they live near the ground. Besides these three species there is one other undescribed species in the east from Florida and the Gulf states and a subspecies of it known only from three specimens, two from New Jersey and one from Long Island. One of the western species has been found in the mountains of western Georgia and may be a race by itself. I have seen only five specimens of it. All the rest are from the middle states and western plains from Manitoba to Texas and Arizona and west to Colorado and Wyoming. So

far none is known from Mexico or Central America. Two, one of which is probably a subspecies of *G. marcassita* (Crotch) and the other *G. pubescens* (Mels.) occur in Washington State, and there is one record of *G. pubescens* from California. A number of species are found in Canada, one of which is described in this paper and known only from Canada.

It seems likely that in the course of time specimens will be collected in Mexico and new ones taken in this country. In the material seen there are isolated specimens or a single series represented. For instance, I have seen only one specimen of *G. obscurus* LeConte, the type, and in this paper have described two species from one specimen apiece. In the case of one group I have so little material that I cannot come to any better conclusion than did LeConte who named them all "*varians.*" They no doubt represent several species. Within almost all the units that I have distinguished as species, there is great variability in size and coloration. Since no real characters to differentiate these variant forms can be found, and since the aedeagi show no great differences, one can only group these diverse-appearing specimens together tentatively under one specific name, after calling attention to the minor differences and hope that sometime greater series may be collected and more biologic work done in observing the hostplants. Another group of which *G. nebulosa* is a representative, appears to have developed some faint characters to differentiate the different races. But whether these races are specific or subspecific one cannot at this stage determine.

Of the three most abundant species, *G. pubescens* is well known to feed on *Oenothera. G. marcassita* breeds on the roots of strawberry, and *G. curtipennis* has been collected by J. C. Bridwell in Virginia on *Hypericum perforatum*, and the Florida subspecies by W. S. Blatchley in Florida on *Asyrum hypericoides,* of the St. Johnswort family (Hypericaceae). A new species here described has been collected in Texas and New Mexico on *Gaura parviflora,* which is related to *Oenothera,* and *G. nebulosa* and *G. varians* are reported by Norman Criddle in Canada on *Oenothera,* and *G. bicolor* from Texas on *Oenothera.* Other than these records we know almost nothing about the hostplants, the few records of the other specimens being apparently chance captures on plants that probably bore little relation to the actual host.

The only life history of any of the species is that by Forbes[10] who made observations on three strawberry rootworms, *Colaspis brunnea* (Fabr.), *Paria aterrima* (Oliv.), and *Scelodonta* (*Graphops*) *pubescens* (Mels.). The last one was so identified by LeConte to whom he had sent his beetles, and who at that time was away from his collection and in failing health and with poor eyesight (he lived not much longer). Forbes later compared the strawberry *Graphops* with the one feeding on *Oenothera* and, questioning the identification of the strawberry one as *pubescens*, sent both to Horn, who identified the *Oenothera* beetle as *pubescens* and the strawberry one as *G. nebulosa* (LeConte). Forbes' drawing, poor as it is, is not that of either *pubescens* or *nebulosa*, and is probably that of *G. marcassita* (Crotch), which is the strawberry feeder. According to Forbes, the strawberry *Graphops* in the latitude of southern Illinois attacks the strawberry roots in August and September, spends the winter as a larva, pupates in May, and emerges as an adult in June. Forbes, finding adults of *G. pubescens* in April on *Oenothera*, was thus led to compare them with the strawberry species and he quickly noted their difference both in habits and in appearance.

I am indebted to the following institutions and men who have freely put their collections before me: W. J. Brown, Dept. of Agriculture, Ottawa, Canada; P. J. Darlington, Museum of Comparative Zoology; R. H. Beamer, University of Kansas; L. J. Bottimer; H. M. Harris, Iowa State College; J. N. Knull, Ohio State University; Hugh Leech, California Academy of Sciences; C. E. Mickel, University of Minnesota; John C. Pallister, American Museum of Natural History; H. C. Severin, South Dakota State College; John A. Wilcox, New York State Museum, and the U. S. National Museum.

Key to Species of GRAPHOPS

1. Pubescence fine and inconspicuous, beetles dark bluish or purplish green, elytral humeri small. Arizona .... *barberi* n. sp.
   Pubescence usually coarse and conspicuous, humeri not notably small 2
2. Front femora with a small tooth 3
   Front femora without tooth 6

[10] Forbes, Psyche, vol. 4, 1884, pp. 123--130, 167-168.

3. Elytra considerably over twice as long as prothorax, densely punctate in basal half of elytra. Widespread ..*pubescens* (Melsheimer)
Elytra approximately twice as long as prothorax or a little more, elytral punctation not dense 4

4. Elytra with a conspicuous patch of white pubescence on either side of the scutellum, elytral punctation coarse. Southeastern states ....*floridana* n. sp.
Elytra without conspicuous patch of white pubescence on either side of scutellum, elytral punctation not coarse 5

5. Punctation on prothorax in transverse wrinkles, strigose. Widespread in eastern and middle U.S. ......*curtipennis* (Melsheimer)
Punctation on prothorax fine and dense but not strigose. Long Island, New Jersey ....*floridana borealis* n. ssp.

6. Beetles dull black without lustre 7
Beetles with more or less lustre and either bronzy, coppery, or metallic blue or green 8

7. Punctation of prothorax dense, round and deep; pubescence fine and evenly distributed. Colorado ....*obscura* LeConte
Punctation of prothorax not so dense or coarse and in clusters with some roundish impunctate areas, pubescence coarse and in thicker patches on elytra. Colorado ....*nigella* n. sp.

8. Clypeus with deep angular emargination 9
Clypeus with shallow wide-angled emargination 13
Clypeus with rounded emargination 18

9. Front of head without transverse impression or sulcus connecting the supraorbital cleft. Elytral punctation dense over entire elytra. Kansas, Oklahoma, Mississippi, Texas *simplex* LeConte
Front of head with more or less evident transverse impression or sulcus connecting supraorbital cleft 10

10. Eyes concealed from above by bulging occiput. Prothorax and elytra with coarse white pubescence, in unrubbed specimens concealing the punctures below. Coppery or bronzy. Texas, New Mexico ....*comosa* n. sp.
Eyes not concealed from above by bulging occiput, pubescence not so dense as to conceal entirely the sculpture beneath. Usually metallic blue or green 11

11. Large (5.5-6 mm.). Prothorax very densely punctate all over and duller than the elytra, deep bluish green. Nebraska, Minnesota, Colorado, Wyoming ....*beryllina* LeConte
Somewhat smaller, shining blue, green, coppery or bronzy. Prothorax not so densely punctate 12

12. Elytra with striate punctures closely set and strong even to the apex. Locality unknown .... *punctata* n. sp.
Elytra with striate punctures not very closely set and becoming much finer and indistinct towards apex. Manitoba, South Dakota, Colorado, Kansas, Missouri, Iowa, Illinois, Georgia *varians* LeConte
13. Tip of aedeagus with a more or less broad end 14
Tip of aedeagus with an acute end 15
14. Aedeagus with a broad blunt tip. Texas .... *exilis* n. sp.
Aedeagus with not so broad but blunt tip. Wyoming *wyomingensis* n. sp.
15. Dull black. Colorado, Manitoba .... *nigella* n. sp.
Metallic blue green, bronzy or coppery 16
16. Metallic blue green. Colorado, W. Kansas, New Mexico, Texas .... *smaragdula* (LeConte)
Bronzy or coppery 17
17. Small. Texas, New Mexico .... *tenuis* n. sp.
Larger. Manitoba, Montana, Wyoming, South Dakota, Colorado, Nebraska .... *nebulosa* (LeConte)
18. Punctation in basal part of elytra dense and somewhat confused, beetle bluish green. Saskatchewan .... *viridis* n. sp.
Punctation in basal part of elytra not dense or confused but striate. Beetle bronzy. Widespread over U. S. and Canada .... *marcassita* (Crotch)

Graphops pubescens (Melsheimer)

Plate 1, Figure 2

Eumolpus pubescens Melsheimer, Proc. Acad. Nat. Sci. Phila., vol. 3, 1847, p. 169.
Heteraspis pubescens LeConte, Col. of Kansas and Eastern New Mexico, Smithson. Contrib., 1859, pp. 23, 24.
Graphops pubescens LeConte, Trans. Am. Ent. Soc., vol. 12, 1884, pp. 26, 27. Horn, Trans. Am. Ent. Soc., vol. 19, 1892, p. 205.

Elongate oblong oval, bronzy black somewhat shiny although faintly alutaceous, with light, unusually fine pale pubescence; prothorax distinctly and densely punctate, elytra with fine striate punctation and in basal half punctures between the striate rows; the elytra unusually long for the genus.

Head rounded over occiput with a distinct shallow frontal depression but no impressed line or sulcus across dividing the

upper from the lower front and connecting the deep sulcus about the eyes; surface alutaceous and distinctly punctate, more coarsely in lower front, the clypeus cut straight across, not at all emarginate; pubescence fine and inconspicuous, nowhere dense. Antennae with rounded basal joint, the last five joints somewhat wider and more pubescent than the short shiny basal joints. Prothorax wider than long with rounded sides, not very convex, surface shiny although faintly alutaceous, and densely and strongly punctate; the punctures in transverse lines on sides and towards the base, slightly pubescent. Elytra elongate, somewhat shiny, faintly alutaceous, the striate punctation not at all coarse and in basal half with finer punctures in intervals, towards apex the punctation becoming fainter; the pubescence fine and inconspicuous. Body beneath densely punctate, lightly pubescent except on sides of metasternum and to a lesser extent on sides of abdomen where the hairs are denser. Femora very finely and inconspicuously toothed, claws with a long inner tooth. Length 3.2 to 4.4 mm.; width 1.5 to 2 mm.

Type in Melsheimer or LeConte collection, Museum of Comparative Zoology. In the Melsheimer collection a female with label "*pubescens* Melsh." and two others with pale blue discs and "Ziegler" on them. In the LeConte collection is one with a pink disc (indicating the Middle Atlantic States), labelled *pubescens* Melsh. in LeConte's handwriting. There are, besides this one, 9 others, 2 with pink discs, 1 from Canada, 4 from New Jersey (not this species but *marcassita*), 1 from Dallas, Texas, and 1 from Texas (not this species). There is also a series on cardboard from New Jersey.

Other localities. Canada: Nova Scotia: Newport, W. J. Brown. Quebec: Joliette, Moznette; Rigaud; Ontario: Toronto, R. J. Crew, Wickham; Brome, W. J. Brown; Constance Bay, W. J. Brown; Meij Bleue, Merivale, Ottawa, all collected by W. J. Brown; Ridgeway, E. P. Van Duzee. Prince Edwards Co. Manitoba: Aweme, N. Criddle. *Maine:* Milford, F. Knab. *New Hampshire:* Mt. Surprise, Intervale, E. L. Bell. *Vermont:* Brattleboro. *Massachusetts:* Boston, Ormonde; Cambridge, Hubbard and Schwarz; Chicopee, F. Knab; Springfield, F. Knab. *Connecticut:* Sheffield Island, J. Zabriski. *Rhode Island:* Newport, W. Robinson. *New York:* Albany; Batavia, H. H. Knight;

Clinton Hts.; Colden, E. P. Van Duzee; Crugers; Cypress Hill; Forrest Park, Schaeffer; Highland Park, Schaeffer; Ithaca, Chittenden; Karner, J. A. Wilcox; Long Island, M. L. Linell, A. T. Slosson; McKeever, J. A. Wilcox; Newport; Palmyra, E. M. Becton; Pelham, L. Lacey; Phoenicia, E. P. Van Duzee; Redford, Schaeffer; Riverhead, L. I., V. M. Kirk; S. Bethlehem, N. K. Bigelow; Sound Beach, L. I.; Suffolk Co., C. V. Relchart; West Point, W. Robinson. *New Jersey:* Bridgeport, Halmbach; Boonton, G. M. Greene; Cape May, F. Knab; Clementon, Kaefer; Clifton, R. Godfrey; Delanco, George Greene; Floral Park; Holly Beach, Halmbach; Lehigh Gap, G. M. Greene; Paterson, J. A. Grossbach; Phillipsburg, J. M. Green; Rutherford, E. G. Lensley; Trenton, E. L. Dickerson; Tuckahoe, J. W. Green; Westwood. *Pennsylvania:* Darby, J. W. Green; Delaware Co., George Greene; Easton, J. W. Green; Glen Olden, George Greene; Hanover, Barber and Bridwell; Overbrook, George Greene; Philadelphia, G. M. Greene; Roxborough, Halmbach. *Maryland:* Baltimore, F. E. Blaisdell; Berwyn, F. C. Pratt; Cabin John, F. Knab; Chesapeake Beach, F. Knab; Glen Echo, J. C. Bridwell; Occoquan, J. C. Bridwell; Plummers Island, E. A. Schwarz; Riverdale, D. H. Blake; Riverview. *District of Columbia:* Woodridge. *Virginia:* Arlington, on *Oenothera biennis* Linn., D. H. Blake, C. H. Popenoe; Charlottesville, L. C. Woodruff; Dead Run, Fairfax Co., R. C. Shannon; Falls Church, G. M. Greene; Fredericksburg, W. D. Richards; Ft. Monroe, Hubbard and Schwarz; Old Point Comfort, D. H. Blake; Portsmouth, I. J. Condit; Nelson Co., W. Robinson; Vienna, W. S. Abbott. *West Virginia:* White Sulphur Spgs., W. Robinson. *North Carolina:* Valley of Black Mts., W. Beutenmiller; Round Knob, Hubbard and Schwarz; Southern Pines, A. H. Manee. *Georgia:* Barnsville, T. L. Bissell. *Louisiana:* Bossier Parish, W. F. Turner. *Mississippi:* Columbus, P. N. Oman; Grenada Co., J. A. Wilcox. *Texas:* Dallas, Houston, J. L. Ward, Wickham; Longview. *Tennessee:* Wickham. *Kentucky. Illinois:* Glen-Ellyn, F. Knab. *Ohio:* Hocking Co., Franklin Co., Fairfield Co., Greene Co., all by J. A. Wilcox. *Michigan:* Big Rapids, N. F. Howard; Detroit, Hubbard and Schwarz; Marquette, B. Notman; Port Huron, Hubbard and Schwarz. *Wisconsin:* Waupaca, L. G. Gentner; Madison, J. E. Dudley. *Iowa:* Ames, Story Co., P.

and C. Vaurie; Iowa City, Wickham, Buchanan; Lake Okoboji, Buchanan. *Missouri:* C. V. Riley; Columbia, W. S. Craig. *Kansas:* Douglas Co., F. H. Snow; Elk City, M. W. Sanderson; Lawrence, L. S. Henderson; Mt. Hope, Wickham; Onaga, Howard Deay; Riley Co., E. A. Popenoe; Topeka, E. A. Popenoe; Winfield, C. E. Burt. *Nebraska:* Omaha, H. Soltau. *Arkansas:* southwest. *Oklahoma:* Muskogee Co., J. A. Wilcox; Payne Co., R. E. Bird. *South Dakota:* Dupree, Chamberlain, Cavour, Vayland, all by H. C. Severin. *Colorado:* Denver, H. Soltau; Greeley, Wickham. *Arizona:* Carrizo, D. J. and J. N. Knull; Oak Creek Canyon, 8000 ft., F. H. Snow. *California:* Castle Crag, A. Fenyes. *Washington:* N. Yakima, Wickham; White Salmon, W. W. Baker.

Remarks. The beetles in the LeConte and Melsheimer collection labelled *pubescens* are the same species, and there is little doubt about what Melsheimer described as *pubescens.* They are distinctive in having proportionately longer elytra than is usual in the genus, and are also unusual in being rather finely and not coarsely pubescent. The head lacks the usual transverse impressed line or depression across the front dividing the upper from the lower front. The distribution of this species is like that of its hostplant, *Oenothera biennis* Linn., widespread over the country, and the beetles present little variation in appearance in their wide range, also an unusual feature in this genus.

Graphops curtipennis (Melsheimer)

Plate 2, figures 1, 2

Eumolpus curtipennis Melsheimer, Proc. Acad. Nat. Sci. Phila., vol. 3, 1847, p. 169.

Heteraspis curtipennis LeConte, Col. of Kansas and eastern New Mexico, Smithsonian Contrib., 1859, pp. 23, 24.

Graphops curtipennis LeConte, Trans. Am. Ent. Soc., vol. 12, 1884, pp. 26, 27. Horn, Trans. Am. Ent. Soc., vol. 19, 1892, p. 205.

Oblong oval, shining with a bronzy or coppery lustre, eyes prominent, pronotum with punctures in transverse lines forming wrinkles, elytra with light pubescence in lines converging towards suture at the apex.

Head with outstanding eyes projecting out from the prothorax,

shiny although faintly alutaceous, with short inconspicuous white pubescence, the pubescence about eyes not as thick as usual in the genus, the punctures a little coarser in lower front than in upper, the division between the upper and lower front marked by a lightly impressed line, not grooved, and uniting with the impressed median frontal line; clypeus nearly straight across, only slightly curved. Antennae as usual in the genus. Prothorax approximately a third wider than long with rounded sides, shiny, the punctures in transverse lines, making the disc wrinkled. Elytra with prominent humeri, rather densely but finely punctate in basal half, the punctures on the side being impressed and wrinkled, in apical half indistinct; pubescence light and short and in lines converging towards suture. Body beneath and legs lightly pubescent and finely punctate. Claws with short inner tooth, front femora with a tiny tooth. Length 2.7 to 3.5 mm.; width 1.4 to 1.8 mm.

Type ? in LeConte collection, Museum of Comparative Zoology, collected in Pennsylvania, by Melsheimer. Hagen [11] wrote of the Melsheimer collection that LeConte took specimens from it which he incorporated into his own collection and according to Hagen they may be recognized by the shorter pin. In LeConte's collection the specimen bearing the name *curtipennis* Mels. has the shorter pin of Hagen's description and bears a pink disc (indicating the Middle States). I believe that this may be regarded as the Melsheimer type. In the Melsheimer collection is a specimen labelled *curtipes* in Hagen's (?) writing to which H. S. Barber has attached the label "type of *curtipennis*." This is not the same species as that in the LeConte collection bearing the short pin. To me it does not seem wise to question LeConte's recognition of this distinctive little species and to attach too much importance to a specimen in the Melsheimer collection of whose history we know so little — a specimen labelled, I believe, by Hagen, which is of approximately the same size and coloration — when we have in LeConte's own collection bearing the label *curtipennis* a specimen undoubtedly of Melsheimer's collection. LeConte in naming specimens has identified this little species with the prominent eyes and wrinkled pronotum as *curtipennis* pretty generally in collections throughout the country, and it has gone under that name for many years undisputed. H. S.

[11] Hagen, Canadian Ent., vol. 16, 1884, pp. 191-197.

Barber insisted that Melsheimer's description of the "transverse arcuated impressed line" on the front of the head applied more to *marcassita* than to this species, but it can well apply to this species too. In fact there are very few in the genus without that line. The description of the pronotum as "minutely punctured and rugulose" certainly applies to *curtipennis*. The specimen labelled *curtipes* has a finely punctate but not at all rugulose pronotum.

Other localities. Canada: Ontario: Toronto, R. J. Crew and A. Fenyes, Normandale, W. J. Brown; Walsingham, W. J. Brown. *Maine:* Monmouth, C. A. Frost. *New Hampshire:* Manchester, W. S. Abbott. *Massachusetts:* Mt. Tom, F. Knab; Springfield, F. Knab. *New York:* top of Mt. Whiteface, J. M. Aldrich; Oswego, Wickham; Karner, J. A. Wilcox. *Connecticut:* Mystic, R. H. Beamer. *New Jersey:* Da Costa, F. Knab; Davisville; Glassboro, W. F. Rapp; Lakewood; Lucaston, G. M. Greene; Sicklerville, W. F. Rapp; Ramsay. *Washington, D. C.:* H. S. Barber, W. A. Donnell, F. H. Chittenden. *Maryland:* Glen Echo, J. C. Bridwell. *Virginia:* Dawson Beach, 4 m. south Occoquan, on *Hypericum perforatum*, J. C. Bridwell; Bull Run, J. C. Bridwell; Virginia Beach, A. D. Hopkins; Ft. Monroe, Hubbard and Schwarz. *North Carolina:* Graybeard. *Michigan:* Midland, R. Dreisbach. *Iowa:* 7 m. n.w. Thompson, G. O. Hendrickson; Ames, G. O. Hendrickson; Sioux City, Slater and Laffoon. *South Dakota:* Bad Lands, Kadoka, Coster, G. I. Gilbertson; 15 m. south Mission, Todd Co., Hicks, Slater, and Laffoon. *Kansas:* Lawrence, Warwick Benedict. *Oklahoma:* Muskogee, J. A. Wilcox. *Arkansas:* southwest. *Mississippi:* Montgomery Co., J. A. Wilcox. *Louisiana:* Pear River, H. Soltau. *Texas:* Belfrage collection.

Remarks. This species has an unusually wide range, occurring from Canada to Texas and from the Atlantic states to the Dakotas and southward. Specimens from the western plain states appear more robust but not otherwise different.

In the South occurs a race that is at least subspecifically different. It is shinier and more coppery and often even metallic green in color, and with more slender, not so broad elytra. H. S. Barber has attached the name "*schwarzi*" to a series collected by E. A. Schwarz at Capron, Florida, and I propose to perpetuate the name as a subspecies of *Graphops curtipennis*.

Graphops curtipennis schwarzi n. subsp.

Type and 7 paratypes, U.S.N.M. Type No. 62347 collected at Capron, Florida by E. A. Schwarz and H. G. Hubbard.

Other localities. Florida: Atlantic Beach, A. T. Slosson; Baldwin, Schwarz; Cedar Keys, Hubbard and Schwarz; Daytona; Enterprise, D. M. Castle, Hubbard and Schwarz; Fort Pierce, on pepper; Gomez; Gainesville, P. T. Riherd; Hilliard, E. G. Wegenek; Jacksonville, A. T. Slosson, Ashmead; Kissimmee, Charles Palm; Lacoochee, J. D. Beamer; Lake Placid, J. G. Monticello; Lake Mary; Lake Lucy; Lakeland; LaBelle; Ormond, A. T. Slosson; Palmdale, Blatchley, on St. Andrews Cross; Pebbly Beach, Jacksonville; Plymouth; Punta Gorda, Hubbard and Schwarz; Rockbluff, M. D. Leonard; Sanford, E. T. Van Duzee; Suwannee Spgs., L. D. Tuthill; Stark, R. H. Beamer; Tampa; St. Petersburg. *Georgia:* Adel, E. G. Wegenek; Clinch Co., N. J. and E. L. Sleeper; Okefenoke Swamp, L. T. Hardy; Tybee Island, Kaebel. *Alabama:* Grand Bay, H. P. Loding; Mobile, H. Soltau. *South Carolina:* Clemson College, J. S. Watts; Ten Mile Station, Charleston, D. H. Blake.

Remarks. In Fall's collection are several specimens of this coppery colored race from Florida that he set aside from the specimens of the northern localities. C. A. Frost has labelled this a new species (without name) in J. A. Wilcox's collection.

Graphops nebulosa (LeConte)

Plate 3, figures 1, 3

Heteraspis nebulosus LeConte, Col. of Kansas and eastern New Mexico, Smithsonian Contrib., 1859, pp. 23, 24.

Graphops nebulosus LeConte, Trans. Am. Ent. Soc., vol. 12, 1884, pp. 26, 27. Horn, Trans. Am. Ent. Soc., vol. 19, 1892, p. 205.

Oblong oval, shining, faintly alutaceous, bronzy or coppery black, with coarse white hairs in patches on both prothorax and elytra, punctation of prothorax irregular with impunctate roundish bare areas near the middle of the disc, and the punctures in places densely congregated making thereby a little depressed area; elytral punctation coarser at base.

Head with the cleft connected across the front by a depressed line, the lower front more coarsely punctate; a median depression

or depressed line in the upper front; pubescence in a pattern, very heavy near the eyes; the clypeus with a rounded, concave emargination verging into a wide angled emargination. Antennae with the six basal joints shining with a bronzy or coppery lustre, the distal joints more pubescent and wider. Prothorax nearly as long as wide, with rounded sides, punctation irregular in groups of thickly clustered punctures and between these roundish bare areas without punctation near the middle of the disc; the pubescence in scattered patches, more regular on the sides. Elytra with coarse striate punctures in basal half, the punctures in the apical half fine and inconspicuous, the first two lines impressed; scattered patches of strong white hairs forming something of a pattern on the elytra. Body beneath with regularly placed dense white hairs, denser on the sides of breast and abdomen. Claws widespread with a short tooth at base. Length 4.8 mm.; width 2.5 mm.

Type, probably a female, and one paratype, also female, in the LeConte collection, Museum of Comparative Zoology, with a green disc. LeConte wrote the locality as "Kansas, near Ft. Laramie," now Wyoming, on the Platte River.

Other localities. Saskatchewan: Great Sand Hills, west of Swift Current, A. R. Brooks; Pike Lake, A. R. Brooks; N. Battleford, N. Criddle. *Alberta:* Taber, E. H. Strickland; Lethbridge, J. H. Pepper. *Montana:* Helena, Wickham. *South Dakota:* Parmelee, G. I. Gilbertson; Buffalo, Fox Ridge, Martin, Hecla, Walker, Yankton, all by H. C. Severin. *Minnesota:* Duluth. *Nebraska:* Sandhills. *Wyoming:* Cheyenne, H. Soltau, E. A. Schwarz, Wickham. *Colorado:* Colorado Springs, 6-7000 ft., Wickham, H. Soltau; Denver, H. Soltau.

Remarks. There is even greater variability in this species group, which in this paper is regarded as composed of *G. nebulosa* (LeConte), *G. smaragdula* (LeConte), *G. tenuis* and *G. nigella* (the last two described here), than in any of the others except *G. varians* LeConte. With our present knowledge it is impossible to say whether these are distinct species or subspecies or mere color forms. LeConte, who described the coppery *nebulosa* and green *smaragdula* as separate species, later came to the conclusion that they were the same. The third species, here described as *nigella,* a black beetle, has been generally confused with *obscura* LeConte. And the tiny bronzy beetle found in

Texas and New Mexico, here described as *tenuis*, may be simply a dwarf race. All four are alike in the head formation, in having a wide-angled clypeal emargination often appearing almost rounded, in the pronotum having roundish impunctate areas, and in the elytral pubescence being in patches of denser hairs. On the other hand, the aedeagi although similar present small differences. And there seems to be some geographic distribution peculiar to each of them. So far the green *smaragdula* appears to occur from Wyoming southward to New Mexico and Texas, and *nigella* has been taken so far only in Colorado (at higher elevations) and Manitoba. The small *tenuis* is from Texas and New Mexico. And *nebulosa*, typical form, is taken in more northern localities, from Wyoming northward, many records coming from Canada.

Graphops smaragdula (LeConte)

Plate 3, figure 5

Heteraspis smaragdulus LeConte, Col. of Kansas and eastern New Mexico, Smithsonian Contrib., 1859, pp. 23, 24.

Graphops nebulosus LeConte, Trans. Amer. Ent. Soc., vol. 12, 1884, pp. 26, 27; Horn, Trans. Amer. Ent. Soc., vol. 19, 1892, p. 205.

Narrowly oblong oval, shining metallic green above, deep bronzy or coppery beneath with the legs also bronzy; alutaceous with regularly placed long white appressed hairs on the sides, rubbed elsewhere; punctation not dense on prothorax, and the striate punctures on the elytra not dense.

Head deeply cut by the groove about the eyes, and a distinct depression across front connecting the cleft, and a slight dent on the vertex; clypeus as in *nebulosa* with rounded or wide-angled emargination; well rounded over the occiput, alutaceous and finely and densely punctate; the pubescence inconspicuous except about the eyes and on the sides. Antennae as usual in the genus. Prothorax not quite so long as wide with rounded sides, shiny, indistinctly alutaceous, strongly but not densely punctate with small roundish impunctate areas; a few white closely appressed hairs on the sides (rest rubbed off?). Elytra distinctly alutaceous but shiny metallic green, the striate punctation well marked but not closely placed, becoming finer after middle; regularly placed

white appressed hairs on the sides, rubbed off on the disc. Body beneath and legs bronzy, abdomen densely but not coarsely punctate, the pubescence thicker on the sides of breast; claws as in *nebulosa*, widespread. Length 4.2 mm.; width 2.2 mm.

Type ♀ a female, with a green disc (habitat as given by LeConte "one specimen found at Ft. Laramie"=Wyoming, on the Platte River), in the LeConte collection, Museum of Comparative Zoology. A second specimen, also with a green disc, is about the same size, with patches of white pubescence on the elytra and small roundish impunctate areas on the prothorax. It is not the bright metallic green of the type, but duller and more bronzy.

Other localities. Colorado: Denver, H. Soltau; Canon City, H. Soltau; Pueblo, H. Soltau; northern Colorado, Wickham; Haswell, W. Benedict. *West Kansas:* Popenoe; Norton Co. *New Mexico:* Willard, Wickham, Casey Collection; Clayton, Wickham; Wiegand Ranch, Fall Collection; Estancia, J. R. Douglas. *Texas:* 4 miles north of Marfa, Barber, Russell, Lattimore.

Remarks. As stated above, the localities for the green *G. smaragdula* appear to be more southern than those for *G. nebulosa.*

Graphops nigella n. sp.

Plate 3, figure 2

Oblong oval, alutaceous dull black, only faintly shining under the abundant rather coarse white pubescence, the pubescence in thicker patches on the elytra; prothorax rather irregularly punctate with areas of close punctation and bare impunctate ones, as in *nebulosa,* the striate punctation of the elytra moderately coarse becoming indistinct apically.

Head dull alutaceous black with finer punctures on upper than on lower front; a shallow transverse depression between the clefts about the eyes, and a median vertical impressed line on the front; clypeus with a rounded emargination that in some specimens appears widely angular; pubescence about eyes long and dense, on vertex forming a pattern. Antennae as usual in the genus. Prothorax not quite so long as wide, evenly convex, rather irregularly punctate with clusters of punctures forming little depressions and bare impunctate areas; pubescence moder-

ately long and conspicuous, radiating from the middle. Elytra dull alutaceous black with striate punctures moderately coarse in basal half, becoming fine and indistinct apically except in the impressed row near the suture; the white pubescence dense and long and tending to be in patches. Body beneath and legs covered with white pubescence that is thicker on the sides of the metasternum and abdomen. Claws widespread with an inconspicuous inner tooth. Length 3.5 to 5.1 mm.; width 1.8 to 2.7 mm.

Type male and 20 paratypes U.S.N.M. Type No. 62346, from Denver, Colorado, H. Soltau; 1 paratype in Museum of Comparative Zoology.

Other localities. Colorado: Denver, also collected by Hubbard, Schwarz, and Wickham; Greeley, Wickham, H. Soltau; Hugo, C. O. Marsh; "Colorado," Charles Palm, American Museum of Natural History. *Manitoba:* Brandon, Wickham.

Remarks. In the LeConte collection under *Graphops obscura* are two specimens from Colorado. They are possibly the source of the confusion regarding the identity of *G. obscura,* the type of which is quite different from these two specimens following it. LeConte may have confused them, because of the black color, with *obscura* as in his brief description of *obscura* he mentions one point that applies to these rather than his first specimen, namely that the pubescence is coarse, which is not the case in the specimen with the label. That specimen is unusual in having as fine pubescence as does *G. pubescens* (Melsheimer), as well as being unusual in the strong dense punctation of the prothorax, which LeConte mentions first in his description. In all the collections examined, the specimens like the ones here described as *nigella* have been labelled *G. obscura* LeConte, and nowhere have I found them rightly placed near *nebulosa.* In fact I am not certain that this may not be merely a color form of *nebulosa* although the aedeagus appears somewhat different, and the general dull black appearance of the beetles is quite unlike the shiny metallic green of *smaragdula* or the coppery bronzy lustre of *nebulosa.*

GRAPHOPS TENUIS n. sp.

Plate 3, figure 4

Narrowly oblong oval, alutaceous but shiny bronzy black, pro-

thorax distinctly and moderately densely punctate, elytra with striate punctures distinct to beyond the middle, finer towards apex; pubescence long, rather coarse and dense and in patches on the elytra.

Head alutaceous but somewhat shiny beneath the coarse white pubescence, pubescence heavy about eyes, upper head finely and moderately densely punctate; a depressed line down vertex and another between upper and lower front, lower front more coarsely punctate, clypeus emarginate with a wide angle verging into a rounded concavity. Antennae as usual in the genus. Prothorax not quite as long as wide with rounded sides, alutaceous but shiny, densely and distinctly punctate with moderately dense, white, closely appressed pubescence. Elytra shiny although alutaceous, without convexities, a slight depression below humeri with the striate punctures larger there, and the pubescence also thicker there, the striate punctures distinct to beyond the middle, finer towards apex; pubescence moderately long and coarse, tending to be denser in patches, as along the base, before the middle and at apex. Body beneath alutaceous and finely punctate with the white pubescence thicker along the sides. Claws with a short basal tooth. Length 3 to 4 mm.; width 1.6 to 2 mm.

Type male, U.S.N.M. Type No. 62340, collected at Alpine, Texas, June 28-30, from the Wickham collection.

Other localities. Texas: 14 miles north of Ft. Davis, July 24, 1945, on *Gaura parviflora*, J. H. Russell; Muslene (?) on morning glory; "Texas," Schaeffer collection; Dalhart, Wickham; Brownsville, May 1943, A. J. Chapmann; Bangs, February 16, 1939, Cristonsen; Galveston, F. H. Snow (Kansas U. collection); San Antonio, F. C. Pratt; "Texas," Belfrage. *New Mexico:* Las Vegas, Cockerell; 11 miles east Tolar, on *Salsola pestifer*, V. E. Romney.

Remarks. This may be a small race of that protean species, *G. nebulosa* LeConte. There is little to separate the two except the smaller size and a slight difference in the aedeagus. It is also very similar to the one here described as *G. exilis* from Victoria, Texas, but in general the pubescence is denser and coarser and the aedeagus is quite different in having an acute tip.

Graphops exilis n. sp.
Plate 2, figure 3

Narrowly oblong oval, bronzy black beneath the white, closely appressed pubescence, the pubescence tending to be denser in places in patches; prothorax finely and densely punctate, elytral striate punctures coarser in basal half, rather indistinct in apical half.

Head shiny, finely punctate above, more coarsely punctate in lower front; a depression, scarcely a groove, between upper and lower front, the pubescence light and inconspicuous except about eyes; the clypeus with a wide angled, almost rounded, emargination. Antennae as usual in the genus. Prothorax not quite as long as wide with slightly rounded sides, finely and rather densely punctate, with sometimes small roundish smooth areas on the disc; pubescence light and inconspicuous and closely appressed. Elytra narrow with small humeri, a slight depression below the humeri in which the striate punctures are larger and the pubescence more marked; the surface shiny, not clearly alutaceous with coarser punctures in basal half becoming fine and inconspicuous in apical half, only the row near the suture distinct and impressed; the pubescence fine, tending to be in denser patches, an area of this along the basal margin, another in the depression below the intrahumeral sulcus and on the undersurface denser along the sides of breast and abdomen. Body beneath alutaceous and very finely punctate with light pubescence. Claws with a short basal tooth. Length 3.4 to 3.9 mm.; width 1.7 to 2 mm.

Type, male, and 3 paratypes, U.S.N.M. Type No. 62339, collected at Victoria, Texas, August 29, 1913, by J. D. Mitchell.

Remarks. This is very similar to *G. tenuis,* described here from Texas and New Mexico, but is in general less conspicuously pubescent with finer hairs. The aedeagus is the only certain means of differentiating the two. In *G. exilis* the aedeagus has a wide tip which is in contrast to the pointed tip of *G. tenuis.*

Graphops obscura LeConte
Plate 1, figure 1

Graphops obscurus LeConte, Trans. Am. Ent. Soc., vol. 12, 1884, pp. 26, 27; Horn, Am. Ent. Soc., vol. 19, 1892, p. 205.

Slender oblong oval, dull black, not shiny, distinctly alutaceous and coarsely and densely punctate, with flatly appressed fine white pubescence; prothorax convex and very densely and moderately coarsely punctate, faintly shiny; elytra with large round striate punctures to beyond the middle, more indistinct towards apex.

Head faintly shining, alutaceous, lightly pubescent, finely punctate above and more distinctly in lower front; a slight depression in upper middle front and between the cleft about eyes, a lightly impressed line; clypeus widely and shallowly angulate emarginate. Antennae with the five basal joints shiny, the distal joints wider and hairier. Prothorax a little wider than long with rounded sides; fairly convex and very densely and for the genus coarsely punctate with round deep punctures; alutaceous, faintly shiny, with fine, moderately dense, short white pubescence. Elytra without any basal callosities, humeri small, and little intrahumeral depression; the striate punctures round and large to beyond the middle, then becoming finer; very alutaceous, not at all shiny, with flatly appressed, not very dense fine white pubescence, evenly distributed and of about the same quality as the pubescence of *G. pubescens*. Body beneath covered with fine white pubescence, thicker on the sides of the breast and abdomen; shallowly and finely punctate; claws with tiny basal tooth scarcely discernible. Length 4.5 mm.; width 2 mm.

Type, a male in the LeConte collection, Museum of Comparative Zoology, labelled "Col."

Remarks. This is a very distinct species, unlike any other that I have seen in its dull, alutaceous, deeply punctate, black surface. There is no other specimen like it in any collection that I have examined and only one in the LeConte collection. Following it are two other specimens of another species, both females, with less alutaceous surface and with coarser pubescence not evenly distributed but in patches. They are described in this publication as *G. nigella* and are closely related to *G. nebulosa*.

Graphops marcassita (Crotch)

Plate 6, figures 1, 2

Heteraspis marcassita Crotch, Proc. Acad. Nat. Sci. Phila., vol. 25, 1873, p. 35.

Graphops marcassitus LeConte, Trans. Am. Ent. Soc., vol. 12, 1884, pp. 26, 27; Horn, Trans. Am. Ent. Soc., vol. 19, p. 205.

Broadly oblong oval, somewhat shiny although alutaceous, bronzy black with finely and not very densely punctate prothorax, and elytra with coarser striate punctures becoming finer towards apex; pubescence not very coarse.

Head alutaceous and densely punctate, the pubescence in the type much rubbed but visible about eyes and on sides, the groove between the upper and lower front connecting the cleft about eyes more or less distinct but variable in its depth in different specimens; above this a wide but shallow vertical impression on the front; clypeus small and concavely emarginate. Antennae as usual in the genus. Prothorax a little wider than long, large in proportion to the whole beetle, and moderately convex, alutaceous and finely and not densely punctate, the punctures near the base in transverse lines, the pubescence much rubbed but a little visible around the sides. Elytra short, broad, the humeri moderately prominent, the strong but not very dense striate punctures becoming finer beyond the middle; surface shiny although faintly alutaceous, the pubescence not very coarse, a depression below the humeral sulcus and in this a more alutaceous area; along lateral margin in apical half the punctation indistinct and a little puckering on the sides. Body beneath with the abdomen shallowly punctate and lightly pubescent, the pubescence heavier on the sides. Claws with a short inner tooth. Length 3.8 mm.; width 1.9 mm.

Type ? a female, in LeConte collection, Museum of Comparative Zoology, labelled "*H. marcassita* Zimm." and with an orange disc (according to Crotch's description from the "Middle and Southern States"). Besides the Zimmermann specimen are three others, two with pink discs (Middle States) and one with an orange disc labelled "J. L. LeConte" with a red type label (fixed by N. Banks?). Below this are 5 other specimens, 3 from Haulover, Florida, which are *G. floridana* described in this paper, and 2 labelled "W. T." (Washington Territory), which are the western subspecies described below.

Other localities. Quebec: Aylmer, W. J. Brown; Brome, W. J. Brown. *Ontario:* Arnprior, Carp, Delhi, Leamington, all by W. J. Brown. *New Hampshire:* Durham, W. S. Abbott. *Massa-*

chusetts: Chicopee, Holyoke, Springfield, all by F. Knab. *Connecticut:* Cornwall, L. B. Woodruff; Milford, F. Knab. *Rhode Island:* Watch Hill, W. Robinson. *New York:* New York City; Highland Park; Ithaca, Chittenden; West Point, W. Robinson; Rockaway Beach, L. I. *New Jersey:* Anglesea; Chester, Halmbach; Hopatcong, Charles Palm; Paterson, G. M. Greene; Wenonah, Halmbach. *Pennsylvania:* Colemanville, at root of strawberry, F. C. Pratt; Delaware River Gap, Wickham; Lehigh Gap, G. M. Greene; Philadelphia, G. M. Greene; Water Gap, Charles Palm. *Maryland:* Beltsville, L. L. Buchanan; Bladensburg, Hubbard and Schwarz; Cabin John, D. H. Blake; Glen Echo, J. R. Malloch; Lake Short, on strawberry; Plummers Island, W. L. McAtee, H. S. Barber, E. A. Schwarz. *Washington, D. C.:* Hubbard and Schwarz. *Virginia:* Arlington, D. H. Blake; Glencarlyn, F. Knab; Great Falls, Occoquan, Vienna, all by J. C. Bridwell. *West Virginia:* White Sulphur Spgs., W. Robinson. *North Carolina:* Valley of Black Mts., W. Beutenmuller. *Tennessee:* Nashville, on strawberry. *Michigan:* Eagle Harbor, Lake Superior. Hubbard and Schwarz; Marquette, Hubbard; White Fish Point, Lake Superior, Hubbard and Schwarz. *Illinois:* Pulaski, S. C. Chandler, reared from strawberry. *Indiana:* Clark Co., Purdue; Pekin, on strawberry. *Wisconsin:* Bayfield, Wickham; Hortney, H. A. Robinson. *Iowa:* Muscatine, on strawberry, C. E. Smith; Ames. *Missouri:* St. Louis, G. W. Brock. *Nebraska:* Dodge. *North Dakota:* Sentinel Butte, K. Cooper. *South Dakota:* Buffalo, Eureka, Kadoka Bad Lands, all by H. C. Severin; Brookings, M. Frederiksen; Black Hills, J. L. Webb. *Wisconsin:* Racine, on strawberry. *Montana:* Kalispell, Wickham; Assiniboine, Hubbard and Schwarz. *Wyoming:* Jackson's Hole. *Colorado:* Custer Co., T. D. Cockerell; Colorado Spgs., H. Soltau; Empire, 8500 ft., Wickham; Leadville, 10,000 to 11,000 ft., Wickham; Leavenworth Valley, 9,000 to 10,000 ft., Wickham; Silver Plume, 9,000 to 10,000 ft., Wickham; Marshall Pass, Wickham. *Manitoba:* Brandon, Wickham; Aweme, N. Criddle; Onah, N. Criddle; Riding Mt. Park, W. J. Brown. *Alberta:* T. N. Willing.

Remarks. In the Melsheimer collection is a small specimen of this species which was labelled by Hagen (?) as "Melsh. *curtipes.*" H. S. Barber has attached to this a label indicating

it is the type of *curtipennis* Melsheimer (see discussion under *G. curtipennis*). This small specimen is one of a number of diminutive size that I have examined that might possibly be a subspecies of *marcassita*. These smaller specimens seem to be from the northeastern states. With the exception of the Melsheimer one, presumably from Pennsylvania, one taken on strawberry at State College, Pennsylvania, and one from Angora, Pennsylvania, the others that I have seen are five from Tyngsboro, Mass., one from "Mass.," one from "New Hampshire," one from Port Williams, Nova Scotia, in the Ottawa collection. In the Blanchard collection, labelled "*nebulosus*" are four from Tyngsboro, Mass., one from Mt. Washington, and one from N. Conway, New Hampshire.

Another race of slightly different appearance is from Washington State. William W. Baker has collected them in numbers there on strawberry. At first H. S. Barber thought that they were a new species, but from his later notes it is evident that he regarded them as a subspecies of the eastern *G. marcassita* which he called:

Graphops marcassita pugitana n. subsp.
Plate 6, figure 3

Shinier, less alutaceous, prothorax more finely punctate with shorter, less conspicuous pubescence than the eastern specimens.

Type, a male and 30 paratypes, U.S.N.M. Type No. 62374, collected at Grand Mound, Washington, on strawberry, in April, May, June, August and October, by William W. Baker. Another series of 10 specimens, taken at Grand Mound, Washington, by Arthur Hanson and W. W. Baker is in the California Academy of Sciences.

Other localities. Washington: Chinook Pass, C. W. Getzendaner; Easton, W. W. Baker; Puyallup, W. W. Baker; Spanaway, W. W. Baker; Rochester, W. W. Baker; Tenino, Hubbard and Schwarz.

Graphops simplex LeConte
Plate 1, figures 4, 5, 6

Graphops simplex LeConte, Trans. Am. Ent. Soc., vol. 12, 1884, pp. 26, 27; Horn, Trans. Am. Ent. Soc., vol. 19, 1892, p. 205.

Oblong oval, moderately shiny, bronzy black, with very short, fine, white pubescence that is in lines on the elytra, and not conspicuous, semierect at apical end of elytra; prothorax moderately densely but not coarsely punctate, elytra with dense punctation, wider than prothorax, with prominent humeri.

Head distinctly alutaceous and finely, not densely punctate, a median depressed area in front, the groove not extending across front but ending in a line with the inner edge of the antennal socket; scanty fine hairs about eyes and on sides of front; clypeus deeply angulate emarginate. Antennae with basal joints shining, distal ones pubescent. Prothorax with rounded sides, shiny although finely alutaceous, densely and not coarsely punctate, a few fine inconspicuous short hairs on sides. Elytra broader than prothorax and with unusually broad squarish humeri, densely and distinctly punctate, the punctures so dense as to seem confused, but regular striae of somewhat coarser punctures faintly discernible; shiny, very finely pubescent, the short fine white hairs being in more or less regular lines and erectish towards the apex. Wings unusually well developed. Body beneath alutaceous but shiny, densely and strongly punctate and with fine, inconspicuous white pubescence. Claws with a long basal tooth. Length 3.9 mm.; width 2.3 mm.

Type, female, in the LeConte collection, Museum of Comparative Zoology, from Lavaca Co., Texas, collected May 27. Two specimens with a similar label are in the U. S. National Museum from the collection of C. V. Riley, which may be regarded as isotypes. Besides the type in the LeConte collection are 7 others, 3 without locality labels, simply numbers (929, 430, 431), and 2 very small specimens with Texas labels, 1 large green beetle from Topeka, Kansas, and 1 small blue-green one with the number 432.

Other localities. Kansas: Ft. Scott, H. Soltau; Riley Co., Popenoe; Topeka, Popenoe; Lawrence, W. J. Brown. *Oklahoma:* Norman. *Mississippi:* State College, J. R. Chamberlain. *Texas:* Brownsville, on *Oenothera* sp., J. C. Bridwell; P. A. Glick; J. Shiller; Corpus Christi, F. C. Pratt; Belfrage collection; Dallas, C. R. Jones; on *Physalis*, W. D. Pierce; Goliad, E. A. Schwarz; Victoria, on *Rudbeckia* sp., J. D. Mitchell.

Remarks. Lefèvre's description of *Scelodontia bicolor* (see page 299) fits this beetle pretty well but the locality "Illinois" does not,

and since the type is not available, I believe it is better to take a name that we are certain of rather than a doubtful one, particularly since no specimen from east of the Mississippi or as far north as Illinois has been seen.

This species is one of the most easily recognized of the genus because of its dense elytral punctation and broad squarish elytra under which the wings are fully developed. As in so many others of the genus there is wide variability in size and color, some specimens being less than 3 mm. long, and in color varying from bright metallic bluish green to bronzy black.

Graphops beryllina LeConte

Plate 5, figure 4

Graphops beryllinus LeConte, Trans. Am. Ent. Soc., vol. 12, 1884, pp. 26, 27; Horn, Trans. Am. Ent. Soc., vol. 19, 1892, 205.

Oblong oval, alutaceous but shiny metallic blue green under the coarse white pubescence; prothorax not very shiny, densely and deeply punctate, the elytra with coarse striate punctures, closely set.

Head with the cleft about eyes almost connecting across the lower front, an impressed line between the upper and lower front, and a lightly impressed median vertical line down the front; front covered with moderately dense punctures, each with a closely appressed white hair. Clypeus deeply angulate emarginate. Antennae dark with the basal six joints having a greenish lustre, remainder wider and more densely covered with pubescence. Prothorax almost as wide as long, alutaceous, not very shiny, the punctures dense and deeply cut in irregular transverse rows radiating from the middle, the intervals forming ridges, more apparent in the basal part; a coarse but not long white pubescence on the sides (?rubbed elsewhere). Elytra alutaceous but shiny metallic blue green, with deep, coarse, closely set striate punctures, and between these rows finer shallower punctures, (? scars from rubbed off hairs); intervals between the striate punctures slightly costate, this being more apparent on the sides and at apex; pubescence closely appressed, moderately long, and not in patches but evenly and not densely covering the elytra. (In the type specimen the pubescence is much rubbed.)

Body beneath densely punctate and with coarse white pubescence, especially thick on the sides of breast and abdomen. Claws with a short basal tooth. Length 5.8 mm.; width 3.2 mm.

Type, a female, in LeConte collection, Museum of Comparative Zoology, from "Col."

Other localities. Nebraska: Sandhills, H. Soltau; Sandhills, northwest Nebraska, Kansas College collection; Alliance, Wickham; Halsey, R. Cushman. *Minnesota:* Fertile, A. G. Richards, H. T. Spieth. *South Dakota:* Aberdeen, Gettesburg, both by H. S. Severin. *Wyoming:* Hulett, Cook Co., C. & P. Vaurie.

Remarks. This is one of the largest species of the genus and is a brilliant metallic blue green or green in color, a robust, coarsely punctate beetle with the white pubescence evenly distributed. There is only one specimen in the LeConte collection. It most closely resembles *G. varians,* but is larger, and the prothorax is more densely and deeply punctate, and not very shiny, and the elytral punctures closer.

Graphops varians LeConte

Plate 4, figures 1, 2, 3, 4; Plate 5, figure 3

Graphops varians LeConte, Trans. Am. Ent. Soc., vol. 12, 1884, pp. 26, 27; Horn, Trans. Am. Ent. Soc., vol. 19, 1892, p. 205.

Oblong oval, shining although faintly alutaceous, blue green with long, white, evenly distributed pubescence; prothorax moderately convex and broad, densely punctate but the punctures not so deep or ridged as in *G. beryllina,* elytra with striate punctation not so closely set as in *G. beryllina,* and becoming fine at the apex.

Head with the cleft about eyes extending well into the front and connecting with an impressed line across front, the clypeus deeply angulate emarginate, lower front a little more coarsely punctate than upper, pubescence long and moderately dense. Antennae as usual in the genus. Prothorax a little wider than long, quite convex, shining, strongly and densely punctate but not in ridged lines. Elytra moderately shiny although alutaceous, the first two striate lines impressed entire length, the others becoming indistinct towards apex. Abdomen strongly and densely punctate; the pubescence thicker on the sides of breast and

abdomen. Length 5 mm.; width 2.8 mm.

Type, ? female, from Kansas, in LeConte collection, Museum of Comparative Zoology. The second specimen, of coppery color, is a female from Texas, and has a closely appressed dense pubescence that completely covers the beetle but not so as to obliterate the punctation beneath. The punctation of the pronotum is not so deep or dense and the prothorax not rounded out at the sides as in the type specimen. The third specimen, without locality label, is a deep dark blue with the pronotal punctation not so strong, and the elytra with long white pubescence. The fourth and fifth specimens from Illinois are coppery with a rosy lustre, and in these also the pronotal punctation is not so strong or dense as in the type.

Other localities. Specimens similar to the type specimen are represented in other collections as follows: *Kansas:* Belvedere; West Kansas, Popenoe; Clark Co., 1962 ft., F. H. Snow; Riley Co., Kimbal. *Missouri. Colorado:* Eckley, R. H. Beamer.

Specimens similar to the type but a little smaller and less heavily pubescent, shining metallic green, from: *Kansas:* Meade Co., R. H. Beamer; Scott Co.; H. O. Deay. *South Dakota:* Hot Springs, Fred Bingham; Gettesburg, Fort Ridge, Newell, all collected by H. C. Severin; Brookings, R. A. Vickery. *Manitoba:* Aweme, N. Criddle, on *Oenothera pallida:* Treesbank, R. D. Bird. *Washington:* Leavenworth (this last locality seems improbable).

Specimens similar to the dark blue one in the LeConte collection from: *Kansas:* Jewell Co., Howard Deay. *Iowa:* Sioux City, Jean L. Laffoon; 7 miles n.w. Thompson, Sargeant Bluff, Oak Grove State Park; 4 miles s. Westfield; 6 miles n.w. Ledyard, all collected by G. O. Hendrickson.

Coppery colored specimens more or less similar to the two from Illinois in the LeConte collection: *Central Missouri:* specimens in the Schaeffer, Riley and Casey collections. *Kansas:* F. H. Snow and A. Fitch collections; Riley Co., Popenoe. *Iowa:* Solon, L. Buchanan.

In addition to these is another race represented by 5 specimens from Georgia in the Museum of Comparative Zoology that are coppery colored, and one from Fall's collection, labelled Kenessa Mt. (? Kennesaw Mt.), Georgia, P. W. Fattig, that is metallic green, but apparently the same race. These are similar to the more

western specimens in having a deeply angulate emarginate clypeus and a similar aedeagus, but they appear broader and more convex.

Remarks. Many more specimens are needed for an understanding of this variant group, together with biological study, before any conclusions can be drawn as to the specific status of the beetles. All of these specimens, although seemingly unlike, appear to have no really distinct structural characters.

The type specimen of *G. varians* is remarkably like that of *G. beryllina* LeConte, but is slightly smaller with a shinier, less densely punctate pronotum in which there is no ridging. The elytral punctation is not so closely set as in *G. beryllina.*

Graphops wyomingensis n. sp.

Plate 6, figure 4

Oblong oval, shining bronzy black under the coarse, moderately dense white pubescence; prothorax strongly but not densely punctate, elytral punctation becoming indistinct towards apex.

Head covered with long white pubescence, distinctly and densely punctate, a median vertical depression on front and a very slight transverse depression between the upper and lower front; clypeus emarginate with a wide angle, not quite a curved concavity. Antennae as usual in the genus. Prothorax a little wider than long with the sides not much curved, not at all bulging at the middle, shining under the white pubescence, faintly alutaceous, strongly but not densely punctate. Elytra with small humeri and slight intrahumeral sulcus, a faint depression running down from this that is more alutaceous than the rest of the surface, the striate punctures not dense or large and towards the apex becoming indistinct; pubescence moderately long, coarse and dense, not in patches but evenly distributed; wings not much longer than elytra and narrow. Body beneath covered with moderately long white pubescence, the abdomen not very distinctly punctate. Claws with an exceedingly small inconspicuous basal tooth. Length 3.6 to 4.1 mm.; width 2 mm.

Type male and 2 paratypes, 1 male, 1 female, U.S.N.M. Type No. 62338, from Laramie, Wyoming. Attached to one specimen is a note by H. S. Barber bearing the annotation " 'Nisw'

in C. F. B.'s handwriting on Laramie label, may mean Niswander, fide Ckll." (presumably the collector's name).

Other localities. 1 specimen in American Museum of Natural History, from Cheyenne, Wyoming, June 13, 1920, at 8500 ft.; 1 specimen in N. Y. State Museum, from Como, Wyoming, Williston, collector.

Remarks. H. S. Barber had set these three specimens apart from the rest as being distinct, although he attached no manuscript name to them. On one is a small note written by him, "Penis much smaller than in *nebulosus* or *obscurus.*" In size they are about the same as *G. marcassita* (Crotch), but are covered with heavier, denser pubescence and the clypeal emargination is more angular, and the prothorax has only slightly curved sides.

Graphops barberi n. sp.

Plate 2, figures 4, 5

Narrowly oblong oval, alutaceous but moderately shiny, metallic blue green, with fine, short, not dense white pubescence; prothorax densely but not coarsely punctate, elytra with striate punctures becoming fine towards apex.

Head well rounded over occiput, a slight median vertical line and a depression between upper and lower front, shiny, the upper part more finely punctate than lower, a slightly rounded wide angular emargination of the clypeus. Antennae as usual in the genus. Prothorax nearly as long as wide, moderately convex, with rounded sides, punctation not very coarse except at sides and on prosternum, there the punctures coarser and more confluent; shining, faintly alutaceous, very little evidence of pubescence. Elytra a little wider in apical half, the humeri small with short intrahumeral sulcus, the striate punctures strong in basal half becoming much finer after the middle; the fine, closely appressed white pubescence rubbed or non-existant in most specimens examined. Undersurface and legs densely punctate, wings small and undeveloped, the pubescence light except on the sides of metasternum; claws with a short basal tooth. Length 4.6 to 5.3 mm.; width 2.4 to 2.6 mm.

Type male and 6 paratypes U.S.N.M. Type No. 62343, from Flagstaff, Arizona, collected in July by H. F. Wickham.

Other localities. 1 specimen from the Schaeffer collection labelled "Arizona." Three specimens in the American Museum of Natural History from Tucson, Arizona. Five specimens in California Academy of Sciences, 4 from "Arizona," Van Dyke collection, and one from Flagstaff, E. Schiffel, in J. W. Green collection; one specimen in the Kansas University collection from Magdalena Mts., N. M., F. H. Snow. Two specimens from Flagstaff, Arizona, A. Fenyes; one from Tucson, Arizona, in Fall's collection.

Remarks. A series of 12 specimens collected on the North Rim of the Grand Canyon, 8,000 to 9,100 ft., by D. Rockefeller in the American Museum of Natural History collection is somewhat unlike the others. The specimens are from 4 to 5 mm. in length and in general a little smaller than the Flagstaff ones, and the elytra are wrinkled in the basal half. The tip of the aedeagus is a little differently shaped also. As in the Flagstaff specimens the wings are small and poorly developed.

H. S. Barber recognized this as new and had attached a manuscript name to it which I have changed in dedicating this species to him.

Graphops comosa n. sp.

Plate 5, figure 1

Oblong oval, shining coppery or bronzy black beneath the dense coarse white hairs that on the elytra are irregularly vittate in pattern; prothorax coarsely and rugosely punctate, elytra with coarse striate punctures becoming finer towards apex.

Head with bulging occiput so that the eyes are not as visible from above as in the other species; covered with dense coarse white hairs over occiput and about eyes, not quite so dense on lower front; alutaceous and finely punctate; the cleft about eyes connected across the front by a faintly marked line and with a median vertical line down the front; clypeus deeply angulate emarginate. Antennae as usual in the genus, the distal joints graying with the thick pubescence. Prothorax somewhat wider than long, the surface shining and with deep coarse and often rugose punctation, sometimes in lines radiating from the centre, and often with depressed areas near the curve of the prosternum;

over this and normally concealing the punctation is a dense, closely appressed white pubescence radiating from the median line. Elytra moderately convex with small humeri and rather poorly developed wings, the striate punctures coarse and closely placed, becoming finer towards apex; pubescence dense, coarse and white and in unrubbed specimens having somewhat vittate appearance. Body beneath and legs similarly covered with dense white hairs. Claws with a long basal tooth. Length 4.5 to 5.5 mm.; width 2.4 to 2.9 mm.

Type, male, and 35 paratypes U.S.N.M. Type No. 62341, collected 18 miles north of Imperial, Texas, July 10, 1949 by J. H. Russell on *Gaura parviflora*.

Other localities. 20 miles east of Pecos, Texas, July 28, 1946 on *Gaura parviflora*, J. H. Russell; 12 miles west of Clovis, New Mexico, July 23, 1945, J. H. Russell; 5 miles south of Melrose, N. M., August 21, 1949, J. H. Russell. One specimen in the Kansas University collection from Midland, Texas, collected July 18, 1927 by L. A. Stephenson.

Remarks. H. S. Barber had recognized this as a new species and had attached a manuscript name to it. It has the heaviest pubescence of any of the genus, the elytral punctation being entirely concealed by the coarse white hairs in unrubbed specimens so that the beetles present a grayish appearance not unlike *Glyptoscelis*. The bulging occiput that nearly conceals the eyes from above is another distinctive character.

Graphops viridis n. sp.

Plate 5, figure 2

Oblong oval, moderately shiny although alutaceous, metallic blue green, the pronotum and elytra (in basal part) strongly and densely punctate, the white pubescence evenly distributed.

Head alutaceous and finely punctate, more strongly punctate on lower front, a median line down front and also a transverse line separating the upper and lower front, the clypeus small and slightly rounded, not angularly emarginate but almost truncate; pubescence moderately dense. Antennae as usual in the genus. Prothorax about a fourth wider than long with well rounded sides, moderately strongly and densely punctate, with

a few small bare areas, the punctures becoming finer anteriorly; a fine short pubescence, not at all concealing punctation. Elytra convex, without much intrahumeral sulcus, the striate punctures in basal part strong and between them numerous finer punctures, surface moderately shiny, metallic blue green, finely alutaceous and with fine white pubescence, evenly distributed and not at all obscuring the punctation. Body beneath finely punctate and with short fine pubescence. Legs bronzy. Claws with a short basal tooth. Length 4.1 mm.; width 2.2 mm.

Type, female, U.S.N.M. Type No. 62342, from Swift Current, Saskatchewan, Canada, collected in September 1882.

Remarks. This beetle with its wide prothorax and its rounded sides, convex elytra and green metallic coloration reminds one of the beetles of the *varians* complex. H. S. Barber has labelled it as *G. varians*, in fact. But it is a smaller beetle and the clypeus instead of being deeply angulate emarginate is almost straight across, and truncate and small. The dense punctation at the base of the elytra is like that in *G. pubescens*, but the elytra are not elongate and narrow as in that species. The head is similar to *G. marcassita* but I have never seen a metallic green beetle of that species nor one with the dense elytral punctation. It is unlike *G. wyomingensis* in not having the pubescence in patches, as well as being a broader beetle.

Graphops floridana n. sp.

Plate 6, figure 5

Oblong oval, faintly shining, black, occasionally with a bronzy gleam, alutaceous, lightly covered with short white pubescence, on either side of the scutellum an oblong patch of denser white hairs; elytra with distinct and moderately coarse striate punctures in basal half becoming much finer towards apex; anterior and posterior femora with a small tooth.

Head dull, alutaceous, finely and densely punctate, a little coarser in lower front, with short, inconspicuous white hairs not very dense; the cleft about eyes not connected across the front by an impressed line or groove; a small frontal depression; clypeus almost straight across, only slightly curved or very widely angulate emarginate. Antennae as usual in the genus.

Prothorax about a fourth wider than long, densely and not coarsely punctate, with punctures tending to be in lines, lightly pubescent. Elytra with prominent humeri and very little intrahumeral depression, the striate punctation distinct, moderately coarse and sparse in basal half and along sides, inconspicuous in apical half; surface distinctly alutaceous, only faintly shining, and with short pubescence, on either side of scutellum an oblong patch of denser white hairs. Body beneath faintly shining, very finely punctate and with fine, not dense white pubescence. Anterior and posterior femora with a small tooth, claws with a short basal tooth. Length 3 to 4 mm.; width 1.5 to 2.2 mm.

Type male and 6 paratypes U.S.N.M. Type No. 62344 collected at Tavares, Florida, July 18 by Hubbard and Schwarz.

Other localities. Florida: Punta Gorda; Bartow, Sumpter Co.; Keys, Orange Co.; N. Smyrna, all collected by Hubbard and Schwarz; Ft. Myers (in American Museum of Natural History); Dunedin, W. S. Blatchley; "Ch. Har.," A. T. Slosson. *Alabama:* Oak Grove, H. Soltau; Mobile, H. Soltau. *South Carolina:* Florence, G. F. Ramwater; Saluda Co., on wild plum, W. P. Turner; Black Beard Is., Wild Life Refuge. Four specimens in Bowditch collection labelled "Fla.," 3 in LeConte collection (1 from Haulover, 2 from Orange Co., Fla.), are placed under *G. marcassita* Crotch. In Blanchard's collection is one from Southern Pines, N. C., collected by A. H. Manee. In the Fall collection is one from Edgewater, Fla. collected by C. A. Frost that Fall has labelled as a new species, without a name. There are 4 other specimens in his collection from Orlando, Fla., D. M. DeLong; Florence, S. C.; St. Simons Is., Georgia, C. A. Frost; and Savannah, Ga.

Remarks. H. S. Barber has labelled this as a new species and given the name *floridana* to it. It is readily recognized by the oblong white patches on the elytra near the scutellum and by the toothed femora and dull black alutaceous elytra. Specimens from Alabama and South Carolina are more finely punctate and in this regard approach the northern subspecies, which is represented by only three specimens, two from New Jersey and one from Long Island, described as

Graphops floridana borealis n. subsp.

Plate 6, figure 6

Oblong oval, faintly shining, alutaceous, bronzy black with densely and finely punctate prothorax and finely striate punctate elytra, with short fine, inconspicuous pubescence. Anterior and posterior femora toothed.

Type, female, U.S.N.M. Type No. 62345, collected at Amagansett, Long Island, by W. T. Davis in September 1910.

Other localities. New Lisbon, New Jersey, May 31, 1937, L. J. Bottimer.

Remarks. Only three specimens of this are known, two from New Jersey and one from Long Island, but all three differ from the southern race in having much more finely and more inconspicuously punctate elytra and in lacking the conspicuous white patches of white pubescence on either side of the scutellum. They seem to be a little smaller, ranging from 2.9 to 3.4 mm. in length.

Graphops punctata n. sp.

Plate 1, figure 3

Narrowly oblong oval, faintly shining although alutaceous, bronzy black, the white pubescence evenly distributed, the pronotum finely and densely punctate, the elytra with distinct and closely set striate punctures visible to the apex; clypeus with deep angular emargination.

Head shining under the white pubescence, finely punctate above and a little more distinctly punctate in lower front, the transverse depression between the upper and lower front distinct and well marked, a slight median frontal dent, clypeus with deep angular emargination. Antennae as usual in the genus. Prothorax about a fourth wider than long with well rounded sides, finely and densely punctate with fine, closely appressed white hairs somewhat feathery in arrangement on the sides. Elytra with small humeri, not much wider than prothorax and about twice as long, faintly shining under the evenly distributed white pubescence, the striate punctures closely set, strong and deep and distinct to the apex. Body beneath densely and strongly punctate, covered with white pubescence which is thicker on

the sides of the metasternum. Claws with an exceedingly small and inconspicuous basal tooth. Length 3.6 mm.; width 1.6 mm.

Type, a male, M.C.Z. Type No. 29350 with a pale pinkish disc (? Middle States).

Remarks. I have seen only one specimen, an old one in the Museum of Comparative Zoology without any locality label. The beetle is unquestionably different from any of the others. It may be recognized by its rather slender elongate shape, the strong dense striate punctures on the elytra, and the deeply angulate emarginate clypeus. The aedeagus is also unique in the shape of the tip.

DOUBTFUL SPECIES

Graphops bicolor (Lefèvre)

Scelodontia bicolor Lefèvre, Ann. Soc. Ent. Fr., (5) vol. 7, 1877, p. 164.

"Minor, breviter oblonga, corpore subtus cum capite, antennarum basi, pedibusque omnino, subcupreo-aenea, nitida, prothorace elytrisque cyaneis. Long. 3-3½ mm.; lat. 1½-1¾ mm. Illinois (Lefèvre coll.).

"Caput subtilissime alutaceum, disperse punctulatum, utrinque supra oculos sulco profundo oblique instructum, in media fronte foveolatim impressum, epistomata antice trianguliter emarginato, mandibulis oculisque nigris. Prothorax paulo latior quam longior, lateribus utrinque rotundatus, sat crebre undique punctulatus, subtillissime transversim strigatus. Scutellum triangulare, apice subrotundatum, in medio punctis nonnullis instructum. Elytra prothorace basi latiora, pubis subtile adspersa, tenuiter sublineatum sat dense punctata. Abdomen crebre undique punctatum, subtiliter albidosericeum. Pedes subelongati, femoribus totis subtus muticis."

This description fits pretty well *Graphops simplex* LeConte with which it has been identified, but because I have not seen specimens from east of the Mississippi River or north of Kansas, I am unwilling to adopt Lefèvre's name for that species.

Graphops cupraea (Provancher)

Metachroma cupraea Provancher, Le Nat. Can., vol. 10, 1878, p. 383.
Scelodonta nebulosa Horn, Trans. Am. Ent. Soc., vol. 13, Monthly Proc., 1886, p. xiv.
Graphops ? pubescens Horn, Trans. Am. Ent. Soc., vol. 19, 1892, p. 206.

"Long. .15 pce. D'une cuivré uniforme dans toutes ses parties, a l'exception du labre et des mandibules qui sont noirs. Tête finement ponctuée, les sillons autour des yeux profonds et convergents au milieu du front, celui-ci avec une ligne fortement enfoncée en avant. Prothorax transversal, fortement arrondi sur les côtés, à ponctuations fines et peu denses sur le disque, plus fortes sur las côtés. Elytres à stries à peine indiquées à la base par les lignes de points, à ponctuations très fines et sans ordre au delà du milieu, leur épipleures aussi ponctuées. Pattes de la couleur du corps. Capturée au Cap Rouge."

H. S. Barber has left the following note about this species: "Horn 1886 [12] says *M. cupraea* Prov. is *Scelodonta nebulosa* Lec., and that he examined the type, but in his revision six years later Horn included *cupraea* doubtfully under *pubescens*. Clavareau 1914 wrongly places both citations in synonymy under *pubescens* omitting the queries while Leng 1920 readopts the questioned synonymy used by Horn."

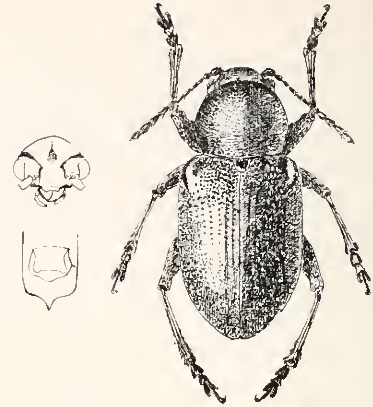
W. J. Brown of Ottawa, Canada, has written me concerning this problem, "Regarding *Metachroma cupraea* Prov., because of the colour of the name label (blue) and the late date on which the species was described, I would expect the type to be in the "second" collection. But there is no specimen in either collection bearing any indication that it is the type. The "second" collection contains three specimens of *Graphops*, two over the label *Heteraspis pubescens* Melsh., one over that of *H.* "*marasitta*" Zimm. All of these are *marcassitus* of our collection, if I am right in believing that only that species and *pubescens* of our collection occur in Quebec. Perhaps Provancher did not return the type to the *cupraea* label after Horn returned it to him (1886, Trans. Am. Ent. Soc., 13, xiv), for there is no specimen with that label now."

In view of the fact that Horn determined the strawberry *Graphops* (*marcassita*) sent him by Forbes as *nebulosa*, it may

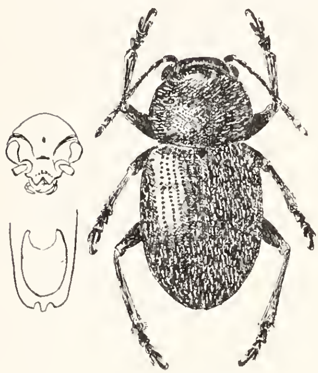
[12] Horn, Trans. Am. Ent. Soc., vol. 13. Monthly Proc., 1886, p. xiv.

be that he did the same in looking at Provancher's *cupraea* and, as Mr. Brown also surmises, Provancher's *cupraea* may really be *marcassita*. On the other hand, the description of the punctation as being very fine and without order to the middle of the elytra seems to be that of *pubescens*.

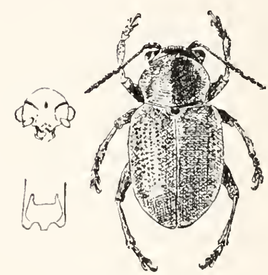
1. Graphops obscura Lec. Type



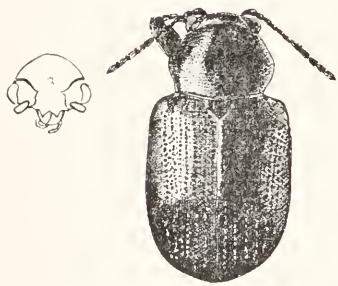
2. G. pubescens (Mels.)



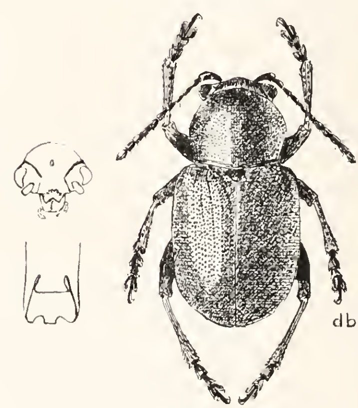
3. G. punctata



4. G. simplex Lec.



5. G. simplex Lec. Type



6. G. simplex Lec.

Plate 1, Figure 1. *Graphops obscura* LeConte, type specimen.
Figure 2. *G. pubescens* (Melsheimer), Hanover, Pennsylvania.
Figure 3. *G. punctata* n. sp. (no locality).
Figure 4. *G. simplex* LeConte, Corpus Christi, Texas.
Figure 5. *G. simplex*, LeConte, type specimen.
Figure 6. *G. simplex* LeConte, State College, Mississippi.

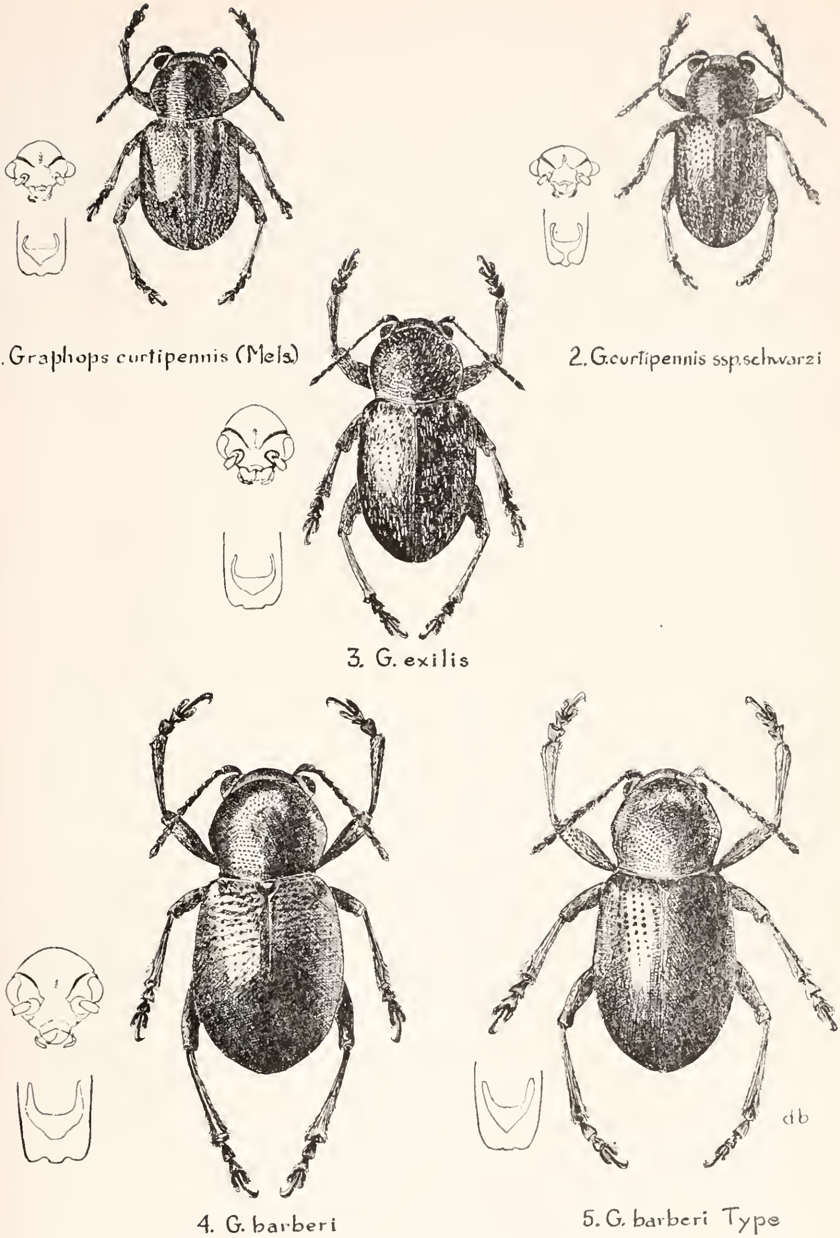


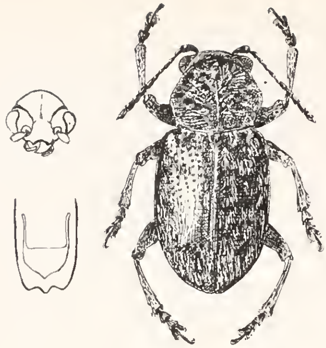
Plate 2, Figure 1. *G. curtipennis* (Melsheimer), Glassboro, N. J.

Figure 2. *G. curtipennis schwarzi,* n. subsp., Capron, Florida.

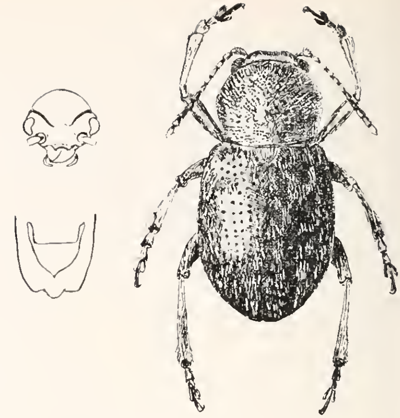
Figure 3. *G. exilis* n. sp., Victoria, Texas.

Figure 4. *G. barberi* n. sp., Grand Cañyon, Arizona.

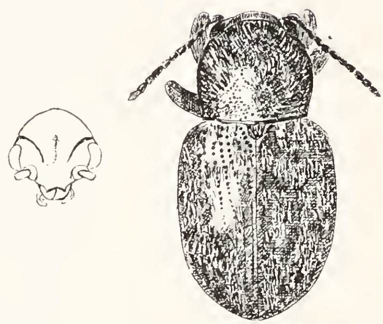
Figure 5. *G. barberi* n. sp., Flagstaff, Arizona.



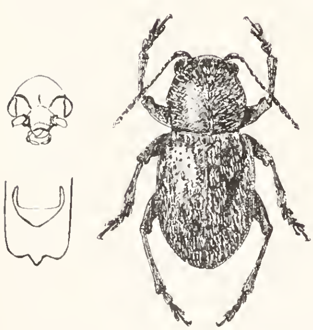
1. Graphops nebulosa (Lec.)



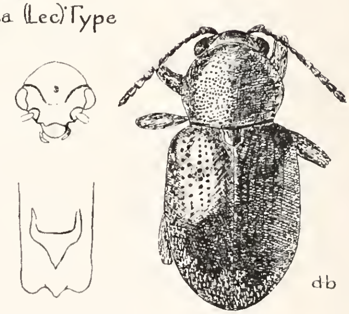
2. G. nigella



3. G. nebulosa (Lec) Type

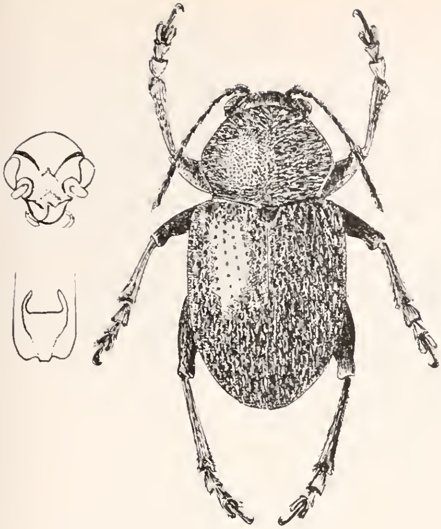


4. G. tenuis



5. G. smaragdula (Lec) Type

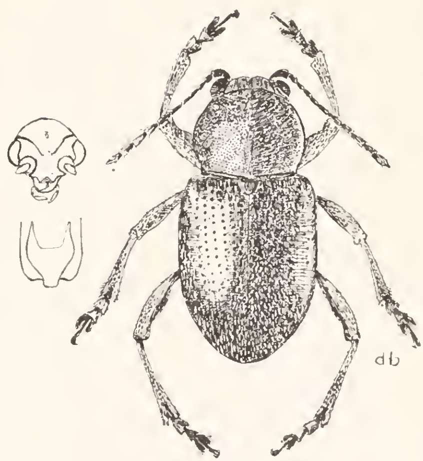
Plate 3, Figure 1. *G. nebulosa* (LeConte), South Dakota.
Figure 2. *G. nigella* n. sp., Denver, Colorado.
Figure 3. *G. nebulosa* (LeConte), type specimen.
Figure 4. *G. tenuis* n. sp., Alpine, Texas.
Figure 5. *G. smaragdula* (LeConte), type specimen. Aedeagus of specimen from New Mexico.



1. Graphops varians Lec.

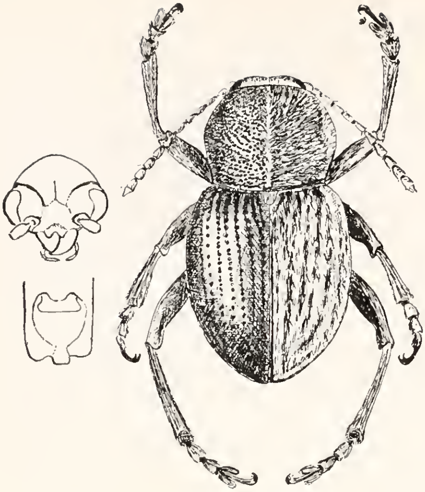
2. G. varians Lec. Type

3. G. varians Lec.

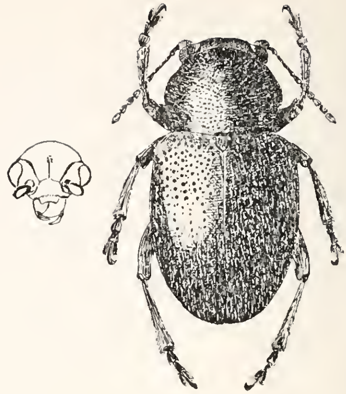


4. G. varians Lec.

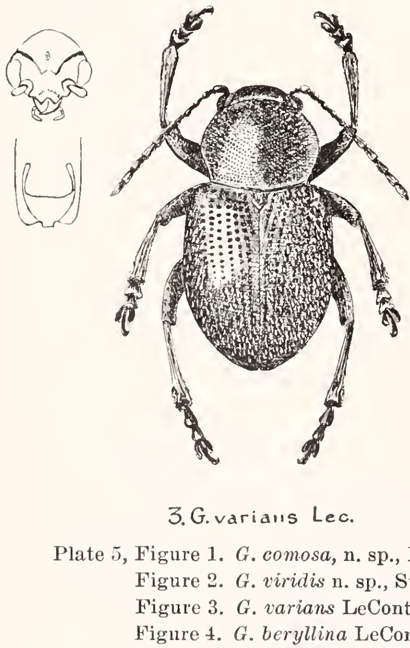
Plate 4, Figure 1. *G. varians* LeConte, Belvedere, Kansas.
Figure 2. *G. varians* LeConte, type specimen.
Figure 3. *G. varians* LeConte, Ledyard, Iowa.
Figure 4. *G. varians* LeConte, Central Missouri.



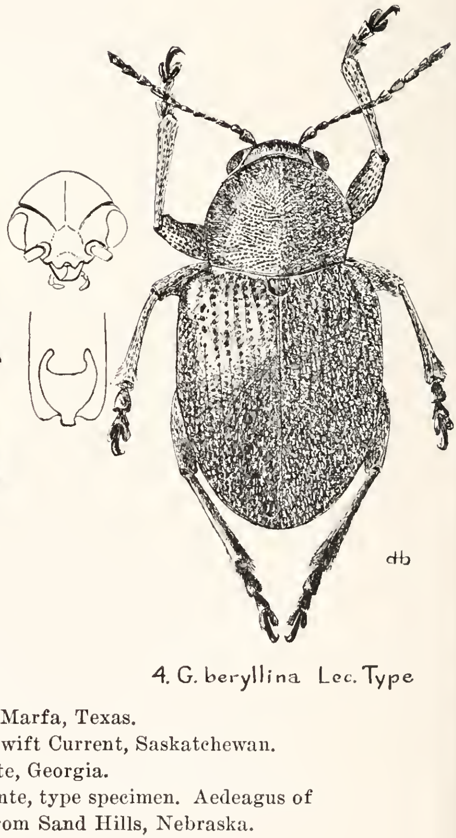
1. Graphops comosa



2. G. viridis

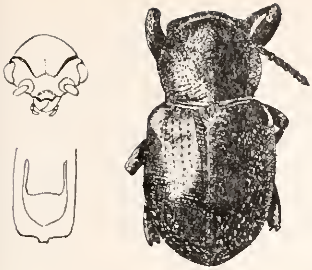


3. G. varians Lec.

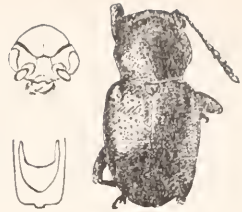


4. G. beryllina Lec. Type

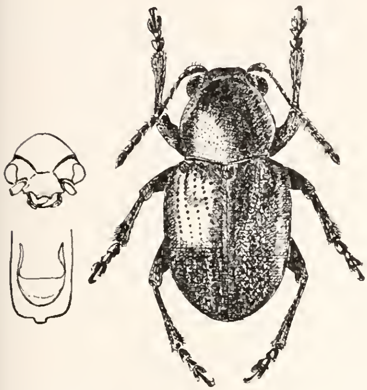
Plate 5, Figure 1. *G. comosa*, n. sp., Marfa, Texas.
Figure 2. *G. viridis* n. sp., Swift Current, Saskatchewan.
Figure 3. *G. varians* LeConte, Georgia.
Figure 4. *G. beryllina* LeConte, type specimen. Aedeagus of specimen from Sand Hills, Nebraska.



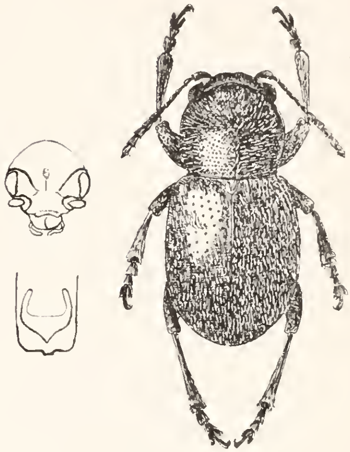
1. Graphops marcassita (Crotch) Type



2. G. marcassita (Crotch)

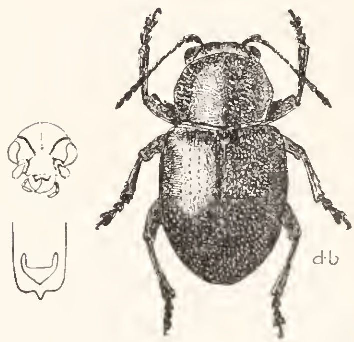


3. G. marcassita ssp. pugitana



4. G. wyomingensis

5. G. floridana



6. G. floridana ssp. borealis

Plate 6, Figure 1. *G. marcassita* (Crotch), type specimen. Aedeagus of specimen from Long Island, N.Y.

Figure 2. *G. marcassita* (Crotch), Melsheimer specimen labelled *curtipes*. Aedeagus of another specimen.

Figure 3. *G. marcassita pugitana* n. subsp., Rochester, Washington.

Figure 4. *G. wyomingensis* n. sp., Cheyenne Pass, Wyoming.

Figure 5. *G. floridana* n. sp., Tavares, Florida.

Figure 6. *G. floridana borealis* n. subsp., Amagansett, Long Island, N. Y.

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AT HARVARD COLLEGE

Vol. 113, No. 5

THE PERMIAN REPTILE ARAEOSCELIS RESTUDIED

by Peter Paul Vaughn

With Two Plates

CAMBRIDGE, MASS., U. S. A.

PRINTED FOR THE MUSEUM

June, 1955

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INTRODUCTION

Williston (1910, 1914) described from the Arroyo beds of the Lower Permian of Texas a small, lightly built reptile, *Araeoscelis gracilis,* which he considered to be an ancestral lizard. *Ophiodeirus casei,* an obviously related form from the somewhat earlier Admiral formation of the Texas Permian, was described by Broom (1913). In 1934, 1935 and 1937, L. I. Price found, in the Belle Plains formation, considerable additional material which corresponds to *Ophiodeirus casei;* comparison of this new material with *Araeoscelis* and with *Ophiodeirus* indicates that the two are congeneric — as suspected by Williston in 1913. This new material has made it possible to describe *Araeoscelis* in more complete fashion and has made it worthwhile to reconsider the phylogenetic relationships of the genus.

My first interest in *Araeoscelis* was aroused by its supposedly very peculiar pectoral girdle, but, in the process of reëxamining this structure, it became apparent that much of this animal's osteology had been unsatisfactorily or inaccurately described. Besides the pectoral girdle, this was particularly true of the palate, occiput, manus and pes. Examination of the materials found by Price and restudy of the specimens available to Broom and Williston have made it possible to reconstruct these parts to a fair degree of completeness and have shown the pectoral girdle to be not so strangely built after all. Further, it has been possible to contribute to our knowledge of the teeth, sacrum, ribs, pelvis and epipodia.

Through reading his papers and as a result of several talks with Dr. D. M. S. Watson, I early became convinced that the structure of the ear would play an important part in the phylogenetic assignation of *Araeoscelis*, and, accordingly, the ear has received considerable emphasis in this paper.

I am greatly indebted to Dr. A. S. Romer at whose suggestion this study was undertaken and under whose inspiring guidance it has been conducted. Dr. E. E. Williams has been a source of encouragement and of many valuable suggestions. I have profited from several stimulating conversations with Dr. D. M. S. Watson. Thanks are due to Dr. E. H. Colbert of the American Museum of Natural History, Dr. J. T. Gregory of Yale University, Dr. E. C. Olson of the University of Chicago, and Dr. R. Zangerl of the Chicago Natural History Museum for extended loans of paleontological specimens; to Mr. A. Loveridge of the Museum of Comparative Zoology for free access to the osteological materials under his care, to Mr. S. J. Olsen for expert instruction in the techniques of fossil preparation, and to Dr. W. L. Brown, Jr. for advice on taxonomic matters. Mr. Elmer Smith, with his eye for form and his skilled draftsmanship, has greatly improved upon my original sketches and has, with admirable patience, coöperated with me in the reconstruction of the skeleton. The greater part of this investigation has been carried on with the financial assistance of a National Science Foundation Fellowship.

History of Description and Systematics. **Williston first** described *Araeoscelis gracilis* in 1910; a humerus and a femur

(figured in 1910) were designated by him as lectotype in 1914. In 1906, Case had discovered, in the upper Admiral, two skulls and associated postcranial material which he believed to belong to Cope's (1878) *Bolosaurus striatus.* Case described these skulls in 1907 and repeated this description, adding a discussion of the postcranial elements, in 1911 as part of a revision of the Cotylosauria. Broom, in 1913, recognized Case's material as different from *Bolosaurus* and set up for it the name *Ophiodeirus casei,* with a skull as type. Williston (1913a) maintained that the postcranial material described by Broom as *Ophiodeirus casei* was actually *Araeoscelis* and (1913b) expressed his suspicion that the skull discrepancy was probably due to error in Broom's description. In 1914, Williston published a more complete description of the osteology of *Araeoscelis,* reaffirming his belief that Case's postcranial material belonged to *Araeoscelis* and stating specifically that it belonged to *A. gracilis.* In this paper, Williston revealed the reason for his unwillingness to positively assign to *Araeoscelis* the skulls described by Broom; Williston, as revealed by a remark on page 376, line 30 of his paper, had misread Broom's description of the skull and had interpreted the antecedent of "it" (Broom 1913, p. 511, l. 20) as *Ophiodeirus* while Broom had actually meant the antecedent to be *Bolosaurus* (see below, under discussion on skull).

The specimens found by Price show that *Araeoscelis* and *Ophiodeirus* are congeneric. Species distinction is, however, desirable in view of the difference in geologic age between the two — the Arroyo material is from the Clear Fork group while the Admiral and Belle Plains specimens are from the Wichita group. In this I follow Romer and Price (1940, p. 11) who advise that " . . . even in cases in which the evidence for morphological distinction is not strong, Wichita and Clear Fork members of a genus should receive different names."

Since the name *Araeoscelis* has priority, the species described by Broom in 1913 is herewith called *Araeoscelis casei* (Broom). This paper then, is concerned with the osteology and relationships of *Araeoscelis* as represented by the two species, *A. gracilis* Williston, 1910 and *A. casei* (Broom, 1913). The synonymy is as follows:

ARAEOSCELIS GRACILIS Williston

Araeoscelis gracilis Williston, 1910, p. 587, pl. 1.

Lectotype. Humerus and larger femur associated with UC[1] 659, 660, 661, 662 and 1708 and figured by Williston in 1910 (Williston 1914, p. 365).

ARAEOSCELIS CASEI (Broom)

Ophiodeirus casei Broom, 1913, p. 510, figs. 2, 3.

Bolosaurus striatus, Case, 1907a, p. 653, figs. 2, 3, 4, 5, *non Bolosaurus striatus* Cope, 1878, p. 509.

Araeoscelis gracilis Williston, 1910; Williston, 1914, p. 377, *partim.*

Holotype. AMNH 4685.

Besides Williston himself, Broom (1931), Watson (figures published in Parrington 1937), Huene (1944a,b), and Romer (1946, 1947a) have published restorations of the skull of *Araeoscelis* based on the specimens found by Williston.

GEOLOGIC OCCURRENCE

Araeoscelis gracilis:

UC 659, 660, 661, 662 and 1708 were collected by Williston in 1910 in a ravine near the west line of Craddock's ranch, in the locality known as the Craddock bonebed, near Seymour, Texas (Sec. 1, S.P.R.R. Co., A-298, Baylor Co.). This locality is in the Arroyo formation of the Clear Fork group, Lower Permian of Texas.

Araeoscelis casei:

AMNH 4685 and 4686 were collected by Case in 1906. He (1907a, p. 653) described the locality as ". . . in a bed of conglomerate . . . near the mouth of Godlin [properly Godwin] Creek, in the northern portion of Archer County, Texas." His American Museum label reads "Fulda ss or just at base, Godlin Creek." Case (1907b) stated that, in the valley of Godwin Creek and in the portion of the valley of the Little Wichita near the mouth of Godwin Creek, the "Fulda" sandstone, which is barren, terminates below in a layer of fossiliferous conglomcrate which separates it from the clay beneath. It may be safely

[1] The following abbreviations will be used throughout the text:
AMNH, American Museum of Natural History
MCZ, Museum of Comparative Zoology, Harvard College
UC, University of Chicago (The full system is actually CNHM UC, the University of Chicago specimens having been transferred, as a gift, to the Chicago Natural History Museum.)

assumed that his specimens were found in the conglomerate below this sandstone.

Sellards (1933) placed the Fulda sandstone (type locality: Fulda, Texas) in the bottommost Clyde.

Case (1907b) gave a map which showed various points at which he had made stratigraphic surveys. One of these points, "XI," near the mouth of Godwin Creek, in Archer County (NE corner, J. J. Lang Survey, A-833, Archer Co.), is the only one, according to the sections Case figured, where the "Fulda" sandstone directly overlies a conglomerate underlain by a clay. This, undoubtedly, is the locality in which AMNH 4685 and 4686 were found.

Comparison of the map given by Romer (1935) with that given by Case shows that Case's "Godlin" ("Godlin" in the text, "Codlin" on the map) Creek is synonymous with "Godwin" Creek of Romer. Case's point "XI" is, according to Romer's map, definitely in the upper Admiral with the lower limit of the Clyde about five miles away. Further, Case (1907b) described the "Fulda" sandstone in the vicinity of Godwin Creek as lying below a clay capped by a "six inch" limestone which Romer (1935; personal communication 1953) takes to be the Elm Creek limestone, the summit of the Admiral. This is the basis for the statement of Romer (1935) that *Ophiodeirus* is present in the upper Admiral. Although Case first named the Fulda sandstone (and assigned the type locality), he appears to have been mistaken in his identification of the sandstone at point "XI." This conclusion is corroborated by the fact that the Clyde, in this region, is a rather unfossiliferous zone (Romer 1935; Romer and Price 1940); Case (1907b, p. 661) described point "XI" 's conglomerate as ". . . frequently so filled with bones that it forms veritable bone beds. . . ."

Case's specimens of *A. casei* may be assigned then, to the upper Admiral of the Wichita group, Lower Permian of Texas.

MCZ 1259 (collected in 1934), 1260, 1261 and 1262 (collected in 1935) were found by Price in Turbeville Pasture, Bar X Ranch, *ca.* 1½ miles west of Williams Ranch, Baylor County, Texas (J. Gibbs Survey, A-566, Baylor Co.). This locality is in the lower portion of the Belle Plains formation, Wichita group. MCZ 1259-1262 constitute the basis for the statement of Romer (1935) that *Ophiodeirus* may be present in the Belle Plains.

The occurrence of *Araeoscelis* may be diagrammed as follows:

	Choza	
	Vale	
CLEAR FORK	Arroyo	*A. gracilis:* UC 659-662, 1708
	Lueders	
	Clyde	
	Belle Plains	*A. casei:* MCZ 1259-1262, 2043
WICHITA	Admiral	*A. casei:* AMNH 4685, 4686
	Putnam	
	Moran	

Materials and Methods. Since the two species of *Araeoscelis* are osteologically indistinguishable, the distinction being maintained only because of the facts of geologic distribution, the discussion will proceed as if a single form were being described. This method seems best because, while enough of the bony elements of both species have been preserved to permit the positive statement of osteological identity, there are many parts for which the materials on hand of either species alone are not sufficient for a complete description. Thus, e.g., the proper reconstruction of the pes depends on a composite study of the specimens of *A. gracilis* and *A. casei.* Further, the interest in phylogeny in this paper rests with comparisons above the level of species. Studies of possible differences between the two species, to be revealed, perhaps, by a detailed analysis of size and proportion, are left to the future.

The Arroyo (*A. gracilis*), Admiral and Belle Plains (*A. casei*) finds of *Araeoscelis* are kept, respectively, at the University of Chicago, the American Museum, and Harvard. The decision that they are all one genus, if not one species, was based chiefly on comparisons in the following structures. Those elements not listed are alike in all the finds but were not considered to be as significant as those listed. Opposite each entry I indicate those

collections which include well preserved material for the study of the particular structure. This listing demonstrates the satisfactory number of significant cross-comparisons between the three collections.

1)	The supratemporal fenestra	All three
2)	Supratemporal	All three
3)	Postorbital	All three
4)	Prefrontal	AMNH, MCZ
5)	Occipital condyle	AMNH, MCZ
6)	Quadrate	All three
7)	Teeth	AMNH, MCZ
8)	Vertebrae	All three
9)	Posterior cervical ribs	AMNH, MCZ
10)	Posterior coracoid	All three
11)	Pubis	MCZ, UC
12)	Humerus	All three
13)	Radius	MCZ, UC
14)	Femur	MCZ, UC
15)	Tibia	MCZ, UC
16)	Astragalus	All three
17)	Calcaneum	All three
18)	Cuboid	All three
19)	Fifth metatarsal	MCZ, UC

UC 659, 660 and 662, each containing the greater part of a postcranial skeleton, are mounted in separate plaster blocks. None of the three has a skull, neck or tail. Each has the dorsal vertebrae, shows a fairly complete ventral view of the pelvic girdle, and includes parts of the anterior and posterior limbs. Only 659 has tarsi. No. 660 has the better part of a pectoral girdle.

UC 661 includes two skulls — one badly broken — and two cervical vertebrae.

Associated with UC 659-662 are five skull fragments, a jaw fragment, isolated vertebrae, parts of both girdles, some complete and some partial specimens of pro- and epipodials, two tarsi with attached metatarsals, and scattered metapodials and phalanges. There are a number of immature pro- and epipodials.

UC 1708 includes many materials not fully prepared although some — a series of vertebrae, an iliac blade, and a tarsus — were figured by Williston. There are mature and immature

vertebrae, some ribs, an immature pelvis and parts of the respective hind limb, a "subadult" pelvis with parts of its hind limb, and parts of various mature and immature limb bones.

AMNH 4685 and 4686 are two distorted but fairly complete skulls. Associated with these skulls are one upper and two lower jaw fragments, a considerable quantity of vertebrae of which some occur in important series, the ventral part of a pectoral girdle, an ischiadic plate, two proximal and one distal portions of humeri, and a tarsus.

MCZ 1259 contains a mandibular scrap, a few incomplete vertebrae, part of a sacral rib, pelvic fragments, and parts of the humerus, femur and tibia.

MCZ 1260 is a laterally flattened skull.

MCZ 1261 is a skull with part of the atlas and the axis attached.

MCZ 1262 is the number given the postcranial parts associated with MCZ 1260 and 1261. These include a fair number of vertebrae of which some occur in series, the better part of one scapulocoracoid and a sizable portion of another, parts of pro- and epipodials, a complete carpus with most of a metacarpus, a "subadult" astragalus, parts of the fourth and fifth metatarsals, and scattered metapodials and phalanges. There is a fragment possibly of a regenerated tail.

MCZ 2043 contains two fairly complete skulls — 2043a and 2043b of this paper — and some jaw fragments. There are two important skull scraps: one, a basioccipital attached to a quadrate and the other, the hind part of a left cheek with attached quadrate, stapes, part of a mandible, part of a pterygoid and crushed braincase parts. There are many vertebrae, some isolated and some in series, and some ribs. There are large parts of both girdles, a sternum, parts of all the pro- and epipodials (there is a complete femur), a complete tarsus, a calcaneum attached to a cuboid, and loose metapodials and phalanges.

The particularly tenacious matrix of all the specimens made it frequently necessary to resort to dental engines, drills and carborundum wheels, but removal of the covering immediately adjacent to the bone was, in almost all cases, accomplished with the use of hand tools. For the detailed examination of the skulls, it was found useful, at times necessary, to stain them with liquids — as anise oil, cedar oil — which increase the contrast

between specimen and matrix. Such oils were particularly valuable in working with the Harvard materials and, without them, it would have been extremely difficult to make out many of the palatal details.

Almost all the figures are composites. Some of the elements, e.g., the carpal bones, were drawn from single specimens, and, in other cases, nearly complete specimens required but the addition of small parts from corresponding materials to present a complete picture — this was true of the humerus, femur, and other elements. All lateral views are from the left side of the body; in some instances, due to the nature of the materials, this involved reversing an original drawing.

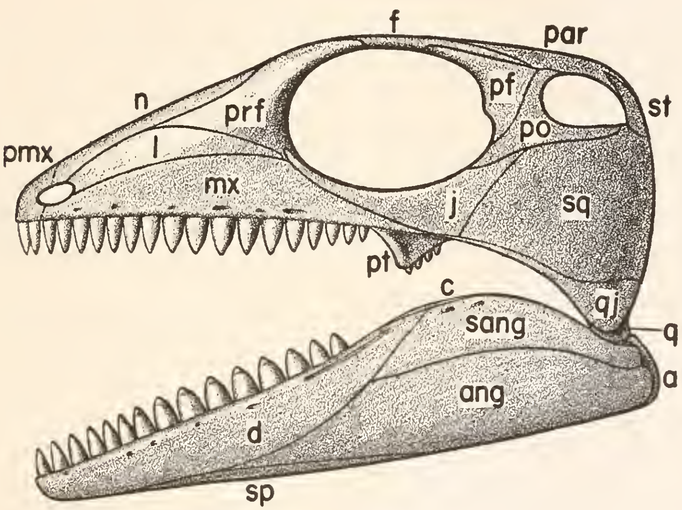

Fig. 1. Lateral view of the skull and mandible. x 2.

OSTEOLOGY

SKULL

(Figs. 1-4)

UC 661 includes two skulls, one of which is badly broken and disarticulated. Associated with UC 659-662 are five skull fragments, two of which are fairly complete; these fragments have been described by Williston (1910, 1914) and figured by Huene

(1944b). AMNH 4685 is a dorsoventrally crushed skull. AMNH 4686 is laterally crushed with the right mandible lifted above the level of the left. There are also two mandibular fragments with the American Museum materials. Both American Museum skulls have been figured by Case (1907b, 1911). MCZ 1259 includes a mandibular fragment. MCZ 1260 is a laterally flattened skull. MCZ 1261 is laterally compressed with the right mandible above the left. MCZ 2043a is crushed both laterally and dorsoventrally. MCZ 2043b is laterally crushed. MCZ 2043 also contains fragments of upper and lower jaws; a fragment of a basioccipital attached to a quadrate; a fragment consisting of the hind part of the left cheek, a stapes, a quadrate and part of a mandible; and the left half of an occipital plate.

By the use of these materials, it has been possible to obtain a composite, fairly complete picture of the skull in which most of the external details of the dermal roof, the occiput, and the palate and the lateral and medial details of the mandible can be made out. Due to severe crushing, it is not feasible, at this time, to present any analysis of the braincase beyond those portions exposed on the palatal and occipital surfaces.

The length of the adult skull is about 42 mm. The largest skulls of *A. gracilis* are equal in length to the largest of *A. casei* although there are several smaller skulls among the *gracilis* materials. The height of the skull (excluding mandible), measured at the mid-point of the orbit, is about 13 mm.; measured through the jaw articulation, the height is about 17 mm. From above the orbit, the skull slopes rather steeply to a height, measured through the naris, of somewhat less than 4 mm. The level of the posterior margin of the skull table is not far ventral to the level of the dorsal margin of the orbit, and the slope between the two is a gentle one. The articulation between quadrate and articular lies considerably ventral — about 4 mm. — to the level of the maxillary dentition.

Measured across its ventral surface, the skull is about 23 mm. wide at the occiput, about 20 mm. at the middle of the orbit, and about 7 mm. at the middle of the naris.

In lateral view, the top of the skull is convex with the described slopes. The ventral margin of the skull is gently concave in the maxillary region and more sharply so in the quadra-

tojugal region where the cheek reaches ventrally to the jaw articulation. The posterior margin of the lateral surface is gently convex. In dorsal view, the lateral margins are gently convex except, of course, for the more pronounced roundness of the premaxillary region. The occiput presents two concavities separated by the median ridge of the supraoccipital. In occipital view, the skull is convex dorsally and laterally, with the greatest curvature in the supratemporal region.

The orbit is large, about 13 mm. long, somewhat of a longitudinal ellipse but nearly circular when sighted along a line perpendicular to its plane — which makes about a 30° angle with the vertical. The center of the orbit lies about three-fifths of the way posteriorly in the length of the skull. The prefrontal, frontal, postfrontal and jugal all enter the orbital border.

The naris is difficult to make out but appears to be a longitudinal ellipse about 3 mm. long, a few millimeters behind the tip of the snout. The lacrimal enters the narial border.

There is a supratemporal fenestra of the type now called "euryapsid." The fenestra is about 6 mm. long and is roughly an ellipse with, however, an acute ventroposterior corner. It is bounded by the postorbital, parietal, supratemporal, and squamosal. The plane of the fenestra is about parallel with that of the orbit.

There is an elliptical pineal foramen, about 2.5 mm. long, bounded by the parietals.

The tall, slim appearance of the skull in occipital view is enhanced by the fact that the quadrates project so far ventrally. The occipital condyle is single and convex; its flat dorsal surface is indented at its posterior end by the semicircular notochordal "pit." The foramen magnum is about 4 mm. in diameter. The posttemporal fenestrae, bounded by supraoccipital, tabular and opisthotic, are somewhat over 2 mm. in diameter. On each side, there is a vertically elongate paraquadrate foramen between quadratojugal and quadrate.

The palate is of the generalized reptilian pattern often referred to as the "rhynchocephalian" type. There is a movable articulation between pterygoids and braincase. There are interpterygoid vacuities of moderate size, small suborbital fenestrae and large subtemporal fossae. The anterior portion of the palate is

so poorly preserved that the size and position of the internal nares can only be guessed at. The most unusual features of the *Araeoscelis* palate are: 1) the placement rather far anterior of the tranverse pterygoid flange and 2) the fact that the quadrate ramus of the pterygoid makes its contact with the quadrate high up, on the dorsalmost part of the latter bone's medial surface.

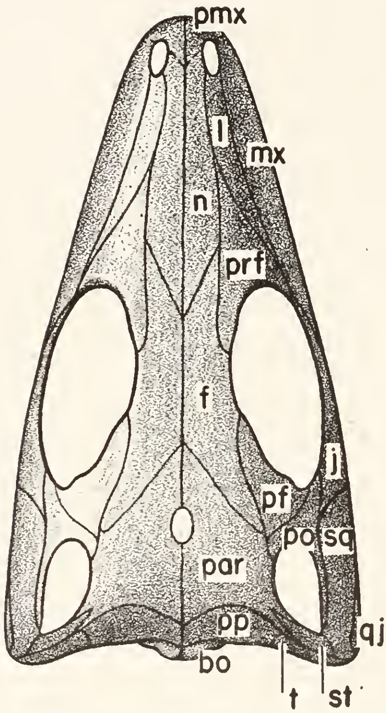

Fig. 2. Dorsal view of the dermal skull roof. x 2.

The high position of this contact (best seen in occipital view) is correlated with the far ventral extension of the quadrate.

The mandible has its greatest height at a smoothly arched coronoid process. From this region, the mandible tapers gently anteriorly and rapidly posteriorly. On the medial surface, there is a large prearticular (Meckelian) fossa but no inframeckelian fenestra. The articular sends a process medially and ventrally

which undoubtedly served as a place of insertion for pterygoid musculature.

The dentition will be discussed separately.

DERMAL BONES OF THE SKULL ROOF (Figs. 1-4)

Premaxillary. This, the least well known bone of the roof, is apparently a small element forming the anterior border of the naris and equipped with the usual nasal and maxillary processes and, presumably, a palatine shelf. The premaxillary of either side seems to have carried two slim, conical teeth. There is no sign of any overhanging, captorhinid-like beak.

Maxillary. The maxillary is the longest bone of the roof, extending from its suture with the premaxillary to its acute contact, below the orbit, with the quadratojugal. It is excluded from the orbital border by the jugal. It forms the ventroposterior border of the naris.

On the lateral surface of the maxillary, just above the gently arched alveolar border, runs a row of small foramina, variable in position and number, which probably served as exits for branches of the superior alveolar nerve and small blood vessels to the labial region.

The alveolar surface of the maxillary bears about seventeen teeth — one more or less; the exact number is difficult to determine. The width of the alveolar surface varies with the serial changes in transverse width of the teeth. This makes for a narrow anterior region followed by a wide intermediate area which gently tapers to an acute posterior termination.

Nasal. From their contacts with the premaxillaries and external nares, the juxtaposed nasals extend posteriorly past the two lacrimals and the two prefrontals to form a wedge which partially separates the two frontals. The apex of this wedge lies somewhat posterior to the anterior limit of the orbit. A transverse section through the nasals presents a dorsally convex outline, giving the snout a rounded dorsal surface.

In dorsal view, the series nasals-frontals-parietals presents an overall picture of an isosceles triangle with a narrow, posterior base.

Frontal. The frontals are spread apart from one another anteriorly by the nasals' wedge, are contiguous interorbitally,

and are separated posteriorly by a wedge formed of the anterior parts of the parietals. A broad mid-portion of the frontal's lateral edge projects between the prefrontal and postfrontal to enter the orbital border.

Parietal. Each parietal abuts on the postparietal of its side in a long, occipitally concave suture, the sutures of the two sides meeting in a posteriorly-directed angle. The lateral edge of the

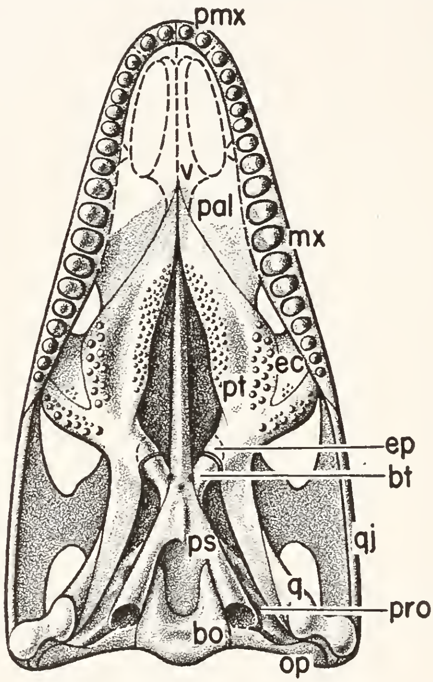

Fig. 3. Palatal view of the skull. x 2.

parietal forms the dorsal border of the supratemporal fenestra.

From its posterolateral corner, the main body of the parietal gives off a long, narrow wing which passes laterally and posteriorly and curves ventrally to touch the squamosal. This wing forms the posterior border of the supratemporal fenestra and, on the occipital surface, lies lateral to the tabular. The wing's external surface is grooved to receive the wedge-shaped supratemporal bone.

The good-sized pineal foramen is enclosed between the two parietals.

Postparietal. The two large postparietals, their common plane meeting the vertical at roughly 45°, form the transition between the skull's dorsal and occipital surfaces. The element is readily identified by its classic, primitive relationships — contacts with parietal, tabular and supraoccipital and separation, by the parietal, from the supratemporal.

Prefrontal. The greater part of the prefrontal is formed into a thick ridge along the anterior border of the orbit. Anteriorly, a sharp prong is forced between the nasal and lacrimal.

Postfrontal. The postfrontal lies along the posterodorsal border of the orbit. Its posterior apex just manages to push between the frontal and postorbital to touch the parietal.

A short process from the postfrontal's anterior edge projects forward into the orbit. A somewhat similar orbital process is seen in some lizards, e.g., *Conolophus, Crotaphytus, Varanus,* where it arises from the postorbital. *Labidosaurus* (Williston 1925, fig. 29) has such a structure too, but it is not clear from which bone it arises.

Postorbital. The postorbital is a triradiate bone. An anteroventral arm extends between postfrontal and jugal to enter the orbital border. A dorsal process, reaching to the parietal, forms the anterior boundary of the supratemporal fenestra, and a posterior proeess lies along the fenestra's ventral border. Superficially, this posterior process seems to exclude the squamosal from all but a minor entry into the fenestral border, but, aetually, this part of the postorbital rests in a depression along the dorsal margin of the squamosal in sueh a way that the squamosal and postorbital, jointly, form almost all of the fenestra's ventral boundary. The postorbital just fails to touch the supratemporal, and so, for a very short distance, the squamosal makes an unaccompanied entrance into the fenestral border.

Jugal. The orbit is bounded ventrally by a long, falciform jugal whose anterior tip is received into a notch in the posteroventral corner of the prefrontal, thus cutting off the lacrimal from the superficial aspect of the orbital rim. The anterior part of the jugal is overlapped by the suborbital portion of the maxillary. The jugal is barred from the ventral margin of the cheek by the long, thin anterior process of the quadratojugal which ex-

tends forward to meet the maxillary.

Lacrimal. From its broad contribution to the narial border the external surface of the lacrimal extends posteriorly, widens, then tapers to terminate near, but not at, the orbital border.

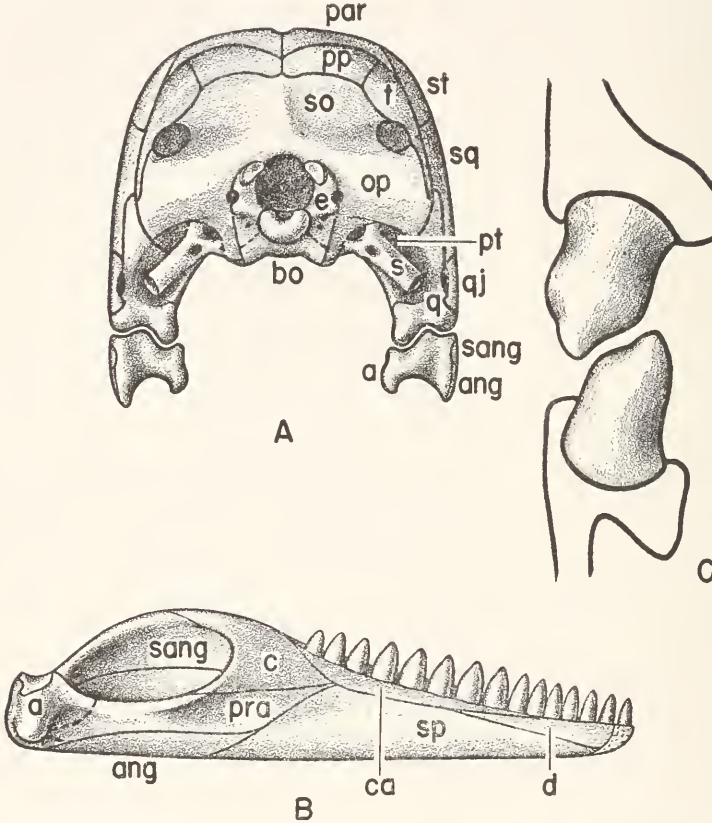

Fig. 4. *A*, Occipital view of the skull (including stapes) and mandible. x 2. *B*, Medial view of the mandible. x 2. *C*, Two teeth, the upper from the maxillary and the lower from the dentary, from about the middle of the alveolar borders of their respective bones. x 7.5.

MCZ 2043a shows, on the anteroventral floor of its right orbit, the posterior end of a bone which contains a good-sized aperture; this piece of bone may represent a part of the lacrimal which lies

internal to the conjoined prefrontal and jugal, and the aperture may be the posterior opening of a lacrimal duct.

Septomaxillary. The state of preservation in the rostral part of the skull does not permit any statement as to presence, absence or form of a septomaxillary.

Supratemporal. There has been enough dispute (e.g., Williston 1914; Broom 1938) over the proper identification of the supratemporal to necessitate some word of justification for the usage in this paper. Since *Araeoscelis* has both supratemporal and tabular — the two elements which are sometimes confused in identification — the matter is greatly simplified. The criteria set up for the supratemporal by Parrington (1937) and Romer (1946) are met by the supratemporal of *Araeoscelis:* it touches the parietal and tabular, is separated from the postparietal by the tabular and parietal, and is separated from the opisthotic by the tabular. These relationships are very primitive, are those found in *Seymouria* (White 1939), and are persistent, changing only with other, gross changes; e.g., the supratemporal may make contact with the opisthotic — but only after loss of the tabular (Romer 1946). Romer also described the supratemporal as sometimes partially wedged into the parietal; this is the case in *Araeoscelis.*

In *Araeoscelis,* the supratemporal is a narrow, wedge-shaped bone which lies, for much of its length, in the groove along the posterolateral wing of the parietal and whose base rests on a depressed facet at the posterodorsal corner of the squamosal. The relationship between supratemporal and parietal is much like that between postorbital and squamosal; the supratemporal and parietal together, the former superficial to the latter, make up the posterior boundary of the supratemporal fenestra.

As already described, the posterior process of the postorbital falls just short of touching the supratemporal below the fenestra.

The supratemporal of *Araeoscelis* has the appearance of a link between the parietal and the squamosal. Its position indicates that it very likely served as a strut, bracing the posterior portion of the roof against the downward pull of powerful temporal muscles.

Tabular. Applying the criteria of Parrington (1937) and Romer (1946), the element about to be described is surely homologous with the tabular in forms like *Seymouria* and *Limnoscelis*

because it touches the parietal, supratemporal, postparietal and opisthotic, helps, along with the parietal, to separate the supratemporal from the postparietal, lies between the supratemporal and opisthotic, and has its dorsal ramus posteromedial to the corner of the parietal.

The tabular of *Araeoscelis* is confined to the occipital surface. Broad in its dorsal part, it is narrow where it forms the lateral boundary of the posttemporal fenestra, and then it tapers to a slender ventral limb which passes, at least superficially, between the squamosal and the paroccipital process of the occipital plate to a limited contact with the dorsalmost tip of the quadrate. The paroccipital process probably met the squamosal deep to the tabular's ventral limb, but it is not possible, with the available materials, to state this as proven fact.

Squamosal. The squamosal is a large plate of bone covering most of the cheek region posterior to the jugal. Its relationships with the postorbital along the ventral border of the supratemporal fenestra have already been described. At its posterodorsal corner, the squamosal bears a facet, which faces laterally, dorsally and posteriorly, for the base of the supratemporal. The gently convex posterior border of the squamosal forms the greater part of the cheek's hind margin.

The squamosal is wrapped around the hind margin of the cheek to present, in occipital view, a narrow, subvertical strip which is in contact with the tabular for its dorsal part, with the quadrate for its ventral part, and, presumably, with the paroccipital deep to the tabular. This strip shows a very distinct step in width, its contact with the tabular lying further medially than its contact with the quadrate.

The squamosal is barred from the ventral margin of the cheek by the quadratojugal.

Quadratojugal. From its main body at the cheek's posteroventral corner, the quadratojugal sends a very slender extension anteriorly along the ventral margin of the cheek to just touch the posteriormost tip of the maxillary below the jugal.

The part of the quadratojugal that is wrapped around the hind margin of the cheek presents a concave medial border which, along with an opposed concavity in the quadrate, forms the vertically elongate paraquadrate foramen. Directly below this foramen, the quadratojugal rests on a special facet cut into the quadrate.

Dermal Bones of the Palate (Figs. 1, 3)

Premaxillary and Maxillary. These two elements possibly contributed small shelves to the dermal palate, but no definite evidence is available.

Vomer. The vomer cannot be made out in the specimens at hand; its probable size and relationships are indicated in the reconstruction.

Palatine. The suture between palatine and pterygoid begins at the suborbital fenestra and runs anteromedially; its anterior termination is unknown. The posterior border of the palatine forms the anterior boundary of the suborbital fenestra. The materials do not permit an examination of the palatine's maxillary and vomerine contacts. Though poor preservation prevents a positive statement, the palatine apparently bore no teeth.

Pterygoid. The pterygoid has the primitive pattern of processes: a palatine ramus, a transverse flange, a quadrate ramus, and a short process directed toward the basipterygoid articulation.

The palatine ramus extends forward from the region of the basipterygoid articulation, widens opposite the suborbital fenestra, and then tapers gently to an acute anterior termination, approximating — just how closely is not clear — its partner of the other side. Along its lateral edge, the palatine ramus borders on the ectopterygoid, the suborbital fenestra, the palatine, and, presumably, the vomer. Its medial edge bounds the interpterygoid vacuity.

The palatine ramus carries two longitudinal ridges, a lateral one and a longer, medial one, with a valley between them. The lateral ridge bears ten to fifteen irregularly arranged teeth, each about 0.5 mm. or so in diameter and not more than 0.5 mm. in height. The medial ridge bears many tiny, unevenly distributed teeth, each about half the size of those on the lateral ridge.

The transverse flange of the pterygoid extends anterolaterally at an angle of about 30° with the transverse plane, passing between the ectopterygoid and the subtemporal fossa to end near the posterior tip of the maxillary to which bone it is tied by the ectopterygoid. The flange is really a thick, subvertical plate whose dorsal margin lies slightly further anteriorly than does its ventral rim. The ventral rim bears seven to eight teeth, each

somewhat larger than those on the lateral ridge of the palatine ramus. The rim also carries a few much smaller teeth scattered in an irregular row just anterior to the large teeth.

The transverse flange slants down laterally and extends ventrally past the lower margin of the cheek to be visible in the lateral aspect of the skull — mouth agape.

The quadrate ramus of the pterygoid is known almost exclusively from its ventral portion, a horizontal shelf which, passing posteriorly from the region of the basipterygoid articulation, arches dorsally, tapers, and comes to lie along the medial surface of the pterygoid wing of the quadrate at a rather high level. Presumably, considering that *Araeoscelis* is primitive in so many other features, the main contact between the pterygoid and quadrate took place via a tall, vertical plate (of the pterygoid's quadrate ramus) which met the lateral edge of the horizontal shelf at a right angle. A trace of this vertical plate is visible on a skull fragment with the MCZ 2043 materials.

The base of the pterygoid's short basicranial process lies somewhat dorsal to the medial border of the palatine ramus. AMNH 4685 indicates that the articulation between the pterygoid and the basipterygoid process of the basisphenoid took place at least partly and perhaps wholly — the immediate region is not very well preserved — via what appears to be the ventralmost portion of the epipterygoid.

Ectopterygoid. The ectopterygoid, visible only in MCZ 2043a, forms the posterior boundary of the suborbital fenestra and ties the transverse flange and the hind part of the palatine ramus of the pterygoid to the maxillary. The ectopterygoid carries several tiny teeth near the middle of its posterior edge.

Parasphenoid. An unpaired, median parasphenoid is definitely present as a discrete, ventral, dermal cover for the basisphenoid and presphenoid. Except for the basipterygoid processes, all of the basisphenoid is hidden from ventral view by this sheath.

In ventral view, the basisphenoidal portion of the parasphenoid is seen to have the general outline of an isosceles triangle with an anterior apex and a posterior base. The long, narrow presphenoidal rostrum of the parasphenoid, its base flanked on either side by a small foramen for the internal carotid artery, passes anteriorly from the apex. From not far behind the apex, two heavy, rounded ridges, broadly confluent anteriorly, diverge and

pass posteriorly leaving a wide, deep valley between them. It is not known whether the basisphenoid contributes to the substance of these ridges; in pelycosaurs (Romer and Price 1940), they are formed by the parasphenoid alone. For want of any other label, it seems best to follow the usage of Romer and Price and call these ridges, inappropriately but conveniently, ''basisphenoidal tubera.''

In AMNH 4685, the posterior part of the suture, on each side, between parasphenoid and basisphenoid can be readily made out on the lateral surface of the braincase at precisely the level at which the convexity of the ''basisphenoidal tuber'' fades into the nearly plane, somewhat medially inclined lateral wall of the basisphenoid. This suture runs anteriorly along the lateral surface of the braincase until it (the suture) curves gently to pass ventrally across the base of the basipterygoid process of the basisphenoid. Thus, the parasphenoid passes between the basipterygoid processes without sheathing them. The material does not permit the suture to be traced beyond the foramen for the internal carotid artery; presumably, it passes dorsally.

The posterior end of the ''basisphenoidal tuber'' presents a shallow, vertically elongate, cuplike depression which faces posteriorly and somewhat laterally. The lateral rim of this cup probably formed the greater part of the anterior margin of the fenestra ovalis.

Though the nature of the contact between parasphenoid and basioccipital cannot be completely satisfactorily analyzed, the basioccipital seems to have sent two lateral prongs into the concave area between the two tubera, each prong apparently applied to the medial surface of the tuber of its side.

A narrow, longitudinal keel, about 1 mm. in height, extends ventrally from the midline of the anterior confluence of the tubera. The anterior limit of this keel lies between the bases of the basipterygoid processes. It is interesting that the smallest parasphenoid among the materials at hand, a specimen in the Chicago collection, has no keel at all; indeed, the site occupied by the keel in larger individuals is depressed in this specimen. The keel may have been variable in development from individual to individual, or it may be that its growth rate was exponential with respect to the growth rate of the surrounding bone. It probably served as a place of insertion for prevertebral muscles.

Directly anterior to the keel, a small but distinct unpaired opening is seen in AMNH 4685, the only specimen in which the immediate area has been well preserved. Although the interior of the braincase is not known, the sella turcica probably lay just anterior to this region of the parasphenoid; the small opening is very likely a remnant of the embryonic passageway through the parasphenoid for the epithelial stalk connecting Rathke's pouch with the oral epithelium. Reference to Gaupp's figures (1906, figs. 382, 383) of the embryonic skull of *Lacerta* will show a closely similar situation. It is not known whether this foramen remained patent in any of the other specimens of *Araeoscelis*. It is interesting that the epithelial stalk remains continuous, passing through the sphenoid bone, in some adult birds (Wingstrand 1951).

There is no suture to indicate that the presphenoidal rostrum may not be a part of the parasphenoid. The rostrum is long and slender, its lateral walls acutely divergent from one another. Its great length in AMNH 4685 suggests that is passed far enough anteriorly to extend, for a short distance, forward above the approximated anterior portions of the pterygoids. There is no manifest suture marking off a presphenoid from the rostrum.

Ossifications of the Palatoquadrate Cartilage (Figs. 1, 3, 4)

Epipterygoid. A fragment of bone possibly part of the epipterygoid can be seen through the supratemporal fenestra of one of the two best skulls with the UC 659-662 materials. This fragment's identification is extremely doubtful, however, and it is not indicated in the reconstruction.

In AMNH 4685, there is seen a slip of bone — very probably the ventral end of the epipterygoid — placed between the basicranial process of the pterygoid and the basipterygoid process of the basisphenoid.

Quadrate. The quadrate is a rather tall element, extending, from its contact with the tabular, far ventrally past the level of the maxillary dentition.

The articular condyle of the quadrate consists of two subhemispherical surfaces — a lateral one and a medial one — separated by a groove. The medial subhemisphere extends farther anteriorly and projects farther ventrally than does the lateral one.

Just above the lateral portion of the condyle, the quadrate bears a small facet for the quadratojugal. Above this, the lateral

border of the quadrate is emarginated for its contribution to the paraquadrate foramen.

A prominent dorsolateral process of the quadrate wedges its way between the squamosal and the paroccipital process to touch the tabular. Anteriorly, the quadrate sends forward a plate-like pterygoid wing whose medial surface is depressed in its dorsal part for a close fit with the posteriorly tapered quadrate ramus of the pterygoid.

The medial surface of the quadrate is channeled by a broad recess which faces upward and inward and extends for a short distance onto the pterygoid wing. Though the posterior surface of the quadrate is convex for all the distance from the tabular to the paraquadrate foramen, it is gently concave in the area between the foramen and the most deeply cut part of the medial recess. The probable functions of the recess and of the depressed area between recess and paraquadrate foramen will be discussed under the section on phylogenetic relationships.

Ossifications of the Braincase (Figs. 1, 3, 4)

Basioccipital. The exoccipitals and the basioccipital are distinguished only with difficulty; the sutures between these bones appear to be represented by two light, symmetrically placed lines which can be made out with the use of oils in AMNH 4685. If these sutures have been correctly determined, the occipital condyle is made up entirely by the basioccipital.

The single occipital condyle is, except for its flat dorsal surface, subhemispherical and is situated at the end of a short pedestal whose sides diverge to flow smoothly into the bone's main body. The notochordal pit takes the form of a semicircular notch cut out of the condyle's flat dorsal surface; this notch is anteriorly continuous with a shallow, median groove running forward on the basioccipital's encephalic surface.

On either side, the lateral portion of the basioccipital is prolonged into a short, ventrally arched, longitudinal ridge. Anteriorly, each ridge is continuous with one of the two prongs of the basioccipital which lie up against the medial surfaces of the "basisphenoidal tubera." Behind this prong, the ridge itself has a short contact with the tuber. Posteriorly, the ridge is in contact with a narrow, plate-like ventral extension of the opisthotic. Between its contacts with the "basisphenoidal tuber" and the

ventral extension of the opisthotic, the lateral surface of each of the two ridges probably helped support the ventral edge of the stapedial footplate, i.e., made up the ventral part of the margin of the fenestra ovalis.

Exoccipital. Each exoccipital has the appearance of a claw whose base rests on the basioccipital, whose concave surface forms the lateral boundary of the foramen magnum, and whose distal tip is directed upward and medially, terminating far short of contact with the exoccipital of the other side. The distal portion of each "claw" carries a proatlantal facet.

Just below the level of the foramen magnum, the exoccipital is pierced by two hypoglossal foramina. The more dorsal of these two foramina faces laterally as well as posteriorly and is situated beneath an overhanging ridge which acts as a buttress for the occipital condyle. Dorsal to the hypoglossal foramina, the exoccipital stands out in relief from the general plane of the occipital plate.

Above the level of the occipital condyle, the lateral margin of the exoccipital is indented by a short, semicircular notch which, with a juxtaposed notch in the opisthotic, forms the jugular foramen.

Proötic, Opisthotic and *Supraoccipital.* The proötic has been made out in ventral view only, and only fragmentary portions are visible. Dorsal and somewhat lateral to the "basisphenoidal tuber," a large foramen — probably for the facial nerve — can be seen. Posterior to this foramen the proötic seems to be produced into a thick ridge directed laterally and somewhat posteriorly. On the ventral margin of this ridge, the proötic, probably in common with the opisthotic, is fluted by a short groove which runs laterally from above the region of the fenestra ovalis. This groove probably received the upper edge of the dorsal process of the stapes. On AMNH 4685, the proötic and opisthotic of the left side have been twisted in such a way that the groove faces posteriorly instead of ventrally.

Though the proötic is not amenable to further study, it probably contributed significantly to the dorsal margin of the fenestra ovalis.

There is no trace of a suture between the fused supraoccipital and opisthotic; as used below, these terms refer to supraoccipital and opisthotic *areas* of the occipital plate.

The supraoccipital bears a median ridge which, beginning just below the suture with the postparietals, passes ventrally, widens, fans out and becomes confluent with the general surface of the bone before reaching the foramen magnum. This ridge probably separated two major areas of fleshly muscular insertion and afforded a line of attachment for a nuchal ligament. The supraoccipital forms the dorsal arch of the foramen magnum.

The lateral process of the supraoccipital makes a broad contact with the tabular and forms the dorsomedial boundary of the posttemporal fenestra.

The slightly recessed, median, ascending process of the supraoccipital lies deep to the medial portions of the postparietals. The main body of the supraoccipital bears a small, obtuse wedge which separates the two postparietals for a very short distance.

Taken together, the two opisthotics present a gently concave posterior surface. The opisthotics, heavier than the supraoccipital, are thin medially but become thicker laterally (in the paroccipital processes).

The widened lateral end of the paroccipital process is in broad contact with the ventral limb of the tabular, with the dorsolateral process of the quadrate, and, presumably, with the squamosal deep to the tabular. The dorsal border of the paroccipital process forms the ventral boundary of the posttemporal fenestra.

The medial portion of the opisthotic's lower edge seems to be drawn out ventrally as a thin, narrow plate which hides almost all of the "basisphenoidal tuber" from the occipital aspect of the skull. This plate cannot be made out satisfactorily on any specimen but is best seen on the right side of AMNH 4685. It apparently formed the posterior wall of the fenestra ovalis.

The suture between opisthotic and exoccipital is interrupted by the jugular foramen.

Basisphenoid. Except for the basipterygoid processes, all of the basisphenoid is hidden from palatal view by the parasphenoid. This condition is by no means unusual but occurs also in, e.g., *Captorhinus* (Price 1935), *Prolacerta* (Camp 1945), *Limnoscelis* (Romer 1946) and *Petrolacosaurus* (Peabody 1952).

The basipterygoid process extends forward and laterally from the main body of the basisphenoid, has a slightly constricted waist, and ends in a moderately convex articular head which faces more anteriorly than it does laterally. The ventral end of

the epipterygoid seems to have been interpolated between the basipterygoid process and the pterygoid.

The suture between basisphenoid and parasphenoid has already been described. The dorsal portion of the basisphenoid cannot be made out, but the foramen for the facial nerve provides an outside limit for its upper border.

The small foramen lying, on either side, in the suture between parasphenoid and basisphenoid at the angle where the presphenoidal rostrum and basipterygoid process diverge, undoubtedly transmitted the internal carotid artery to the sella turcica.

Stapes (Fig. 4). The description of the fenestra ovalis might be summarized at this point. The greater part of the fenestra's anterior margin seems to have been formed by the rim of the cuplike depression at the end of the "basisphenoidal tuber." Again, it is not known whether this contribution is purely parasphenoidal or whether the basisphenoid might not have helped to make up the substance of the tuber. The most dorsal part of the anterior margin is formed by the basisphenoid as an independent element. Ventrally, the fenestra was apparently bounded for a short distance by the basioccipital. The posterior margin of the fenestra was formed by the plate-like ventral extension of the opisthotic. Though no evidence is available, the proötic probably entered the fenestral border dorsally.

The position and boundaries of the fenestra ovalis in *Araeoscelis* are much like those seen in *Captorhinus* (Price 1935) and *Limnoscelis* (Romer 1946). The situation in pelycosaurs (Romer and Price 1940) is closely similar too, but the basioccipital seems to have been barred from the fenestral margin by a downward growth of cartilage from the opisthotic; there is, of course, no assurance that this did not happen in *Araeoscelis* also.

There is a stapes *in situ* on one of the two best skulls with the UC 659-662 materials, and there is a better, displaced one attached to an MCZ 2043 skull fragment.

The stapes is a stout bone, far bulkier than that of lizards and roughly comparable to that of pelycosaurs and *Captorhinus*. Medially, the stapes has a ventral, fenestral process and a dorsal process. The fenestral process, narrower than is the shaft, passes medially along the horizontal to be inserted, as a moderately expanded, concave footplate, into the fenestra ovalis. Near its medial end, the posterior surface of the fenestral process is pierced

by a small, probably nutrient, foramen. Though the details of construction of the thin dorsal process cannot be made out, it is quite obvious that its upper end must have been articulated in the groove along the common ventral edge of the conjoined proötic and opisthotic; this is demonstrated by the manner in which the MCZ 2043 stapes fits the partial fenestra ovalis and groove of AMNH 4685.

The stapedial shaft, a vertical ellipse in cross-section, passes laterally, ventrally and posteriorly to direct its distal end toward the hind part of the medial recess in the quadrate — a recess which we may, following the usage of Watson (1953), call the stapedial recess. The stapes does not quite touch the quadrate but the rugosity of its distal end indicates that it was continued in cartilage. The stapes *in situ* on the Chicago skull has part of its distal end actually in the stapedial recess, and, even though the MCZ 2043 stapes has been displaced to lie along the occipital edges of the squamosal and quadrate, its distal end still lies near, practically in, the recess. These particular relationships will receive further discussion under the section on phylogeny.

Shortly lateral to the base of the fenestral process, the shaft is perforated just above its ventral margin by a large foramen which must have carried the stapedial artery.

Immediately lateral to the stapedial foramen, there is a very small protuberance on the shaft's ventral edge. This protuberance may have served as a place of attachment for a ligament corresponding to the much broader ligament which was attached to the ventral border of the pelycosaurian stapes.

MANDIBLE (Figs. 1, 4)

Articular. The suture between articular and prearticular can be distinguished only on MCZ 2043a and then only with difficulty. It will be best if the terms, as used here, are understood as referring to articular and prearticular *areas.*

The surangular and angular just fail to hide from lateral view the thin sliver of articular which gives the mandible its convex posterior end. Most of the lateral surface of the articular is flat, but there is a distinct lip where it overhangs the surangular for a short distance along the latter bone's dorsal border.

Medially, the articular forms part of the posterior boundary of the prearticular fossa. A short, stout process extends ventrally

and somewhat medially to end in a blunt tip, probably for the insertion of pterygoid musculature.

The articular surface conforms to the condylar surface of the quadrate. Its medial portion lies forward of and ventral to its lateral portion.

Prearticular. The prearticular passes forward between the prearticular fossa and posterior coronoid above and the splenial below to terminate anteriorly in an acute apex which seems to have just touched the anterior coronoid. The conjoined edges of the prearticular and posterior coronoid are drawn out medially to form a short shelf, most pronounced immediately anterior to the prearticular fossa, which overhangs a depressed area of the prearticular.

Dentary. The lateral surface of the dentary extends from the mandibular symphysis to the crest of the coronoid process, tapering back over the splenial, angular and surangular in a long suture which is gently concave dorsally. A line of foramina for labial nerves and vessels runs along the lateral surface just ventral to the alveolar border; in at least one specimen, the most posterior of these foramina is continued externally as an elongate groove.

Medially, the dentary is exposed as a narrow wedge between the anterior parts of the splenial and anterior coronoid.

The dentary seems to have carried about fifteen teeth.

Splenial. The splenial makes up the greater part of the anterior half of the mandible's medial surface. It is wrapped around the ventral edge of the mandible to be presented laterally as a thin splint underlying the dentary and angular.

Angular. The angular has a large lateral exposure and is wrapped around the ventral edge of the mandible to form a narrow strip underlying the prearticular. Its lateral lamina forms the lower half of the lateral wall of the prearticular fossa.

Surangular. The surangular is shorter and narrower than the angular. It forms the upper part of the lateral wall of the prearticular fossa and most of the fossa's dorsal rim.

The line of foramina along the dentary's lateral surface is continued onto the surangular.

Coronoids. There are two coronoids, both edentulous. The anterior coronoid is a narrow element which seems to have tapered to an acute anterior termination without reaching the symphysis.

The posterior coronoid forms the anterior boundary and part of the dorsal rim of the prearticular fossa. It is barred from (at least superficial) contact with the splenial by the narrow meeting between anterior coronoid and prearticular. A very thin splinter of the posterior coronoid was apparently exposed in lateral view atop the mandible's coronoid process.

DENTITION (Figs. 1, 3, 4)

The teeth of *Araeoscelis* have large pulp cavities. They are not labyrinthine. There occur, along with the Harvard materials, a few small, isolated jaw fragments which contain teeth very obviously labyrinthine. I have, however, prepared several thin sections through teeth which definitely belong to *Araeoscelis,* and these sections demonstrate quite conclusively that *Araeoscelis* is not even remotely labyrinthodont. Besides this, the labyrinthine teeth may be distinguished from those of *Araeoscelis* by the slight recurvature of the former.

The implantation of both upper and lower teeth is of the shallow, "subthecodont" type. In both the upper and the lower jaw, the labial walls of the sockets are high and the lingual walls low. The wall of the dentary lateral to the row of teeth is wider than the corresponding wall of the maxillary. The lateral cusps of the upper teeth came to approximate this wall of the dentary when the mouth was closed. There is little space between successive teeth.

It is not possible to determine the exact number of teeth, but a close study of all the available materials indicates the following very probable counts: each premaxillary carried two teeth, each maxillary seventeen and each dentary fifteen.

Considering the upper jaw first, the teeth exhibit striking serial changes in structure. The anterior two-fifths or so of the teeth are slim pegs with conical, pointed tips. Passing posteriorly, the teeth undergo a transverse broadening which gradually increases, reaches a peak somewhat more than halfway along the maxillary, and then decreases again so that the posteriormost several teeth resemble the anterior ones in width (although not in height — the anterior teeth are much taller). Along with the increase in transverse width, the teeth also take on a lateral, pointed cusp whose distinctiveness on each particular tooth seems to be roughly proportional to that tooth's transverse width. This cusp is set off

fairly sharply from the medial portion of the tooth's distal surface; there is a less pronounced, rounded step between the cusp and the lateral surface of the tooth's main body.

The teeth of the dentary show the same serial changes that those of the upper jaw do, but with three differences: 1) There are fewer teeth in the lower jaw. 2) The cusps of the lower teeth are medial, rather than lateral, structures. 3) The medial edge of the cusp is smoothly confluent with the medial surface of the main body of the tooth.

The upper teeth are directed somewhat laterally, the angle of inclination being more marked in the more broadly widened teeth — in these teeth the angle with the vertical reaches about 20°. The lower teeth also show a serial gradient in inclination, the difference being that they point medially; the angles are the same as for the upper jaw. When the mouth was closed, the lateral cusps of the upper teeth approximated the wide labial wall of the dentary, thus hiding the lower teeth from lateral view. The lower teeth, however, did not approximate the maxillary bone.

The materials do not approach the adequacy required for a thorough analysis of the occlusion; they do suggest, however, that occlusion was not simply a matter of an upper tooth to a lower tooth but that, in at least some places, a tooth of one jaw met two of the other.

Most of the specimens seem to have died with full sets of teeth, the few missing teeth apparently having been lost post-mortem. The only case in which teeth seem to be lacking with any kind of serial regularity is in one of the UC 661 skulls where, in the left upper jaw, there are three gaps separated by intervals of two teeth apiece; there is, however, no sign of any similar condition in the right upper jaw. Although a few small jaw fragments show places at which large teeth are followed by smaller ones, in all of the larger, more complete specimens, the tips of almost all the teeth of a jaw bone lie very nearly in a straight line; it seems doubtful that there was any ragged, wave-like replacement. Presumably, as in edaphosaurs (Romer and Price 1940), *Araeoscelis* had a very rapid mode of tooth replacement.

Out of seven specimens in which the anterior members of the maxillary dentition can be seen, only two, one clearly and one not so clearly, show any indication of the development of "canines." MCZ 2043b has, in either upper jaw, a tooth near the

anterior limit of the maxillary which is considerably thicker, though not longer, than its immediate fellows. AMNH 4685 seems to show a similar condition, but the tooth in question is preserved only on the left side, and all but the base has been lost. This sort of heterodonty may, of course, indicate a sexual dimorphism.

With the materials at hand, the description of the palatal dentition cannot be extended beyond that already given.

Comparison With Previous Interpretations Of The Skull

The important descriptions of the skull of *Araeoscelis* given prior to this paper are those of Case (1907a, 1911), Williston (1914), Broom (1913, 1931), Watson (figures published in Parrington 1937), Huene (1944a, b), and Romer (1946, 1947a).

Since it has been thought that dental differences distinguish *Araeoscelis gracilis* from *A. casei,* the teeth might well be discussed first.

Case had identified specimens of *A. casei* as of *Bolosaurus striatus* and, since the teeth of his materials of *A. casei* did not easily lend themselves to study, his description (1907a, 1911) is essentially that of the dentition of *B. striatus.* He even included a figure (1907a, p. 657, fig. 6) of a toothed jaw of *B. striatus* as illustrative of what he thought his materials of *A. casei* looked like. Case's descriptions and plate, since they have nothing to do with the teeth of *Araeoscelis,* are useless in the present consideration.

Broom (1913, p. 511) pointed out that the teeth of *A. casei* (*O. casei* of Broom) are considerably different from those of *B. striatus.* He noticed that ". . . the anterior teeth are round, and the posterior ones are flattened, giving the crown a narrow transverse surface with two low subequal cusps and a shallow valley between them." In a general way, his description fits the present one although the cusps are hardly "subequal" and there is no "shallow valley;" Broom admitted that "In none of the teeth is the crown fully displayed. . . ."

Unfortunately, Broom was guilty of vague reference in his description of the teeth of *B. striatus;* he had referred to *B. striatus* in one sentence and then referred to it again in the next sentence as "it" (p. 511, l. 20). The description which follows

"it" is very obviously of the teeth of *B. striatus,* but Broom's ambiguity confused Williston.

Williston (1914, p. 376) described the teeth of *A. gracilis* as ". . . all simple, without accessory cusps of any kind. They are somewhat wider at the base than long antero-posteriorly and are beveled on the inner side. They are somewhat flattened on the outer side and are obtusely pointed. They are thecodont or protothecodont." After personal examination of the materials available to Williston, I cannot see any basis for the sweeping statement that *all* the teeth were simple and without cusps. The teeth of which he had a good crown view are anterior and posterior teeth, and these, indeed, are simple, but he could have had no good crown view of the middle portion of the tooth row. Inspection of the bases of the middle teeth — the crowns lost — in one of the UC 661 skulls reveals transverse widths and anteroposterior lengths which agree with those described for the middle teeth in this paper. The teeth of *A. gracilis* cannot be completely described without considerable destruction of the too few specimens. There is, however, certainly no evidence which indicates any dissimilarity between the teeth of *A. gracilis* and *A. casei.* This, coupled with the fact of complete concurrence between the two species in all anatomical features in which both are known, renders it almost certain that no dental differences of any significance exist.

Williston mistook the antecedent of "it" in Broom to be *A. casei.* To quote Williston (p. 376): "This [Williston's] description in the main seems to agree with that given by Broom [footnote reference to Broom 1913] of *Ophiodeirus,* though some effort is required to understand his description. One does not feel sure, for instance, what the antecedent of 'it' is in the twentieth line of his description of the teeth, but I assume that it refers to *Ophiodeirus.*" Therein lies the source of subsequent confusion! Williston, however, must have worried further about the matter since he says (p. 377), "There can be scarcely a doubt that, aside from the skull, the bones described by Dr. Broom as of *Ophiodeirus casei* are those of *Araeoscelis gracilis,* and in much probability the discrepancy of the skull is due to error." The damage had been done though, and Williston's distinction between the teeth of *A. gracilis* and those of *A. casei* became the key method of differentiation; Romer (1947a, p. 22) says "*Ophiodei-*

rus . . . is a closely related [to *Araeoscelis*] type from an earlier (Wichita) horizon in Texas. Considerable undescribed material in the Harvard collections indicates that it is almost identical with *Araeoscelis* in every respect except the dentition; the cheek teeth bear an accessory cusp, suggestive of supposedly related Triassic forms.''

Previous descriptions of the skull, exclusive of the dentition, will be discussed chronologically. Only the major differences between these interpretations and mine will be pointed out; minor variations and most areas of agreement will not be mentioned.

Case (1907a) published three halftones of the American Museum specimens of *A. casei:* a lateral view of AMNH 4686, a palatal view of AMNH 4685 (mistakenly labeled ''4686''), and a restoration of the occiput. He also presented a diagrammatic sketch of the AMNH 4685 palate (again labeled ''4686''). Case did not attempt much restoration; detailed comparison is, therefore, rather difficult. He felt (p. 655) that ''. . . there was a complete roof with no trace of temporal vacuities.'' I have found a distinct supratemporal fenestra on each side of the AMNH 4685 skull. Case considered the skull ''. . . roughly triangular in form. . . .'' It is, but the base is much narrower in proportion to the altitude than Case thought it to be. The more nearly equilateral look of Case's specimens is due to post-mortem crushing. Case estimated the number of upper teeth to be sixteen; the specimen on which he probably based this count seems to have had seventeen teeth and is, moreover, definitely less mature than are the larger Harvard specimens on which the greater count of the present paper is based. Case found (p. 656) ''. . . no trace of a foramen quadratum''; this lack is due to crushing. Case did not see the stapedial recess — obvious on AMNH 4685. He drew the posttemporal fenestrae much too large. He did not see the suture between parasphenoid and basisphenoid; the correct oils bring this suture out in AMNH 4685. Case was unable to find any trace of the foramina for the internal carotids in the parasphenoid but admitted (p. 657) that ''. . . these may be very obscure because of their minute size and the condition of the surface of the bone.''

In 1911, Case published diagrammatic interpretations of his halftones of 1907 and labeled as a displaced jugal what seems quite definitely to be a displaced postorbital.

Williston (1914) published figures and a lengthy description of the skull of *A. gracilis*. The suture between frontal and parietal is not the straight transverse line that he thought it to be. It is difficult to see how Williston could have failed to discern the post-parietals — quite obvious on two of the skulls available to him; he must have considered them as parts of a fractured occipital plate. The bone Williston called "tabulare" is, for the reasons I have given, really the supratemporal. He felt that a postfrontal-jugal contact excluded the portorbital from the orbital border; this is not the case. He did not recognize a quadratojugal. I disagree with Williston's reconstruction of the lacrimal in that, as he has drawn it, it enters the orbital border superficially and is a very short element, not even remotely approaching the naris. Williston thought that a paraquadrate foramen might have been present. He did not recognize the stapedial recess in the quadrate. He did not include posttemporal fenestrae in his reconstruction, but this was due to the poor quality of the occiputs in his materials.

Williston's figures have the supratemporal fenestra rather too long and, due to distortion in his specimens, do not sufficiently emphasize the ventralward prolongation of the quadrate.

Broom (1913) limited his description of the skull of *A. casei* almost entirely to differences in dentition between this species and *Bolosaurus striatus*. As we have already seen, and as we shall see again under the discussion of the pelvic girdle, a major fault of Broom's paper is that it is frequently not clear whether a statement refers to *A. casei* or to *B. striatus*. Broom, himself, must have been confused for, having just pointed out that "*Ophiodeirus*" and *Bolosaurus* are distinct from one another, he went on to say (p. 513), with reference to *Bolosaurus*, that "The occiput is closed in at the sides there being so far as I can make out no openings such as figured by Case." Case's figure (1907a, fig. 5) of the occiput was clearly labeled as taken from AMNH 4686 — a specimen which Broom (p. 511) had specifically determined as of "*Ophiodeirus!*" The posttemporal fenestrae can be quite easily made out on AMNH 4685 though they are not nearly as large as Case drew them. Seeing that Case mislabeled AMNH 4685 as "4686" in two other drawings — an error he corrected in 1911 — it is quite possible that his figure of the occiput is incorrectly labeled too. Broom did not see the very distinct

supratemporal fenestrae of AMNH 4685; this is not at all surprising since this region of this particular specimen had received almost no preparation before the present study was undertaken.

In 1931, Broom published dorsal and lateral views of the skull of *Araeoscelis* based on his study of the *A. gracilis* materials. Broom, as did Williston, called the supratemporal the tabular. His reconstruction disagrees with those of Williston and the present analysis in barring the frontal from the orbital border. His restoration of the lacrimal is not significantly different from Williston's. Broom recognized a quadratojugal and felt the squamosal to be excluded from the cheek's ventral margin, but he drew the jugal as partly responsible for this exclusion. He saw that the postorbital enters the orbital border but underestimated this bone's contribution to the boundary of the supratemporal fenestra. Broom's reconstruction (as do all later reconstructions) has the quadrate prolonged further ventrally than has Williston's. Broom restored the squamosal with a gently concave hind border; the small notch he saw at the lower end of this border is a postmortem defect. He recognized the presence of a pair of large postparietals but failed to note the true tabulars.

Watson (figures published in Parrington 1937) prepared lateral and dorsal views of the skull and a medial view of the lower jaw, using the *A. gracilis* materials. Watson identified the supratemporal as such. He thought the lacrimal reached the naris but also restored it as entering the superficial orbital border. He recognized the quadratojugal, tabular, and paired postparietals. Like Broom, Watson figured the frontal as excluded from the orbital border, and, like Williston, he excluded the postorbital too; unlike Williston, Watson attributed this latter exclusion to the intervention of the postfrontal alone. Watson depicted the hind border of the squamosal as gently concave.

All the restorations are correct, in a general way, in their placement of the elements dentary, surangular and angular. Watson was the first author to attempt a restoration of the lower jaw's medial aspect. He was able to see only the posterior portion, and this he drew as essentially correct except that the coronoid is taller than figured, and the coronoid process is more smoothly confluent with the mandible's general dorsal border.

Huene (1944a) redrew Broom's 1931 reconstruction with two major changes: he recognized the "tabular" of Broom as the

supratemporal and noted the presence of a pair of true tabulars. The same year (1944b), he published his sketches of some of the *A. gracilis* skull fragments, labeling the various elements, and repeated Williston's figures, labeling the supratemporal correctly and adding the paired postparietals and tabulars.

Writing on *Limnoscelis,* Romer (1946) made the first attempt at a reconstruction of the complete occiput of *Araeoscelis,* using, besides the specimens of *A. gracilis,* some of the materials of *A. casei* to this end. Romer labeled the supratemporal as such and detected a pair of tabulars. He differs from all other authors, however, in his restoration of the postparietal as a median, unpaired element. His interpretation of the occipital plate is basically correct, but the occipital condyle is placed too far ventral to the plate's lower edge. The quadrate, as he has drawn it, lacks the stapedial recess.

Romer (1947a) based his reconstruction of the skull's dorsal and lateral aspects on the materials of *A. gracilis* alone. He again restored the postparietal as a single, median element. To quote (pp. 21-22) : ''A triangular median element, ridged vertically in the mid-line, appears to be a postparietal — single, as is apparently the case in most if not all reptiles in which adequate data is present. Lateral to this there is, I believe, a highly developed tabular extending far outward to a point opposite the tip of the supratemporal. Watson and Huene interpret this sheet of bone as forming both tabular and paired postparietals; however, the material . . . suggests to me that the supposed suture in this region is a crack.'' In MCZ 2043a (*A. casei*), there is a small piece of bone near the place in which Romer drew a median postparietal, and it might, on first sight, be interpreted as the right half of such an element. However, a suture between right postparietal and right tabular can be made out to the right of this piece of bone. This piece of bone is the right half of a median, ascending process of the supraoccipital, shaped much as is the homologous process in *Captorhinus* (Price 1935). The postparietal of the right side has been pushed, post-mortem, anterior to this ascending process but in life must have lain superficial to it. Between the ascending process and the main body of the supraoccipital is a groove for the ventral edge of the postparietals — again as in *Captorhinus.* This groove might easily be mistaken for a suture between the supraoccipital and a median post-

parietal. The shape of a well-formed postparietal on the left side of AMNH 4685 shows the improbability of a triangular element's being intercalated between two such bones.

Romer's reconstruction agrees with those of Williston and the present analysis in the frontal's contribution to the orbital border. Like Watson, Romer drew the lacrimal as extending from orbit to naris. His interpretations of the postorbital and quadratojugal are essentially like Broom's. As did Broom, Huene and Watson, Romer thought the hind margin of the cheek to be concave; he is alone, however, in depicting the slope of this margin as so far removed from the vertical.

Romer was the first to recognize the role of the splenial on the mandible's lateral surface.

Due to inadequate preservation, none of the reconstructions based on the *A. gracilis* specimens was able to include a satisfactory description of the palate (Williston gave a sketchy description.). Case presented diagrammatic figures of the palate of *A. casei* as found, but the present paper contains the first detailed account of the region.

VERTEBRAE AND RIBS

(Figs. 5, 6)

Despite certain specialized modifications of the *Araeoscelis* vertebral column, its elements are of an essentially primitive type. All the centra, excepting the first, are amphicoelous, and all (excepting perhaps again the first), even those of the elongate cervicals, are notochordal, the notochordal canal constricted midway in its passage through each centrum. Though lateral fossae impart an X-shaped aspect to the neural arch in dorsal view, the arch's swollen, basically cotylosaurian build is still apparent. The articular areas of the zygapophyses are simple, plane surfaces although somewhat tilted from the horizontal; there are no accessory intervertebral articulatory processes.

There seem to have been about thirty-one presacral vertebrae; this estimate is based on a fairly sure number of twenty-two for the dorsal series and a probable count of about nine for the cervicals. The calculated length of the cervical series is about 104 mm.; the calculated length of the dorsal series is about 176 mm.; the calculated and measured glenoacetabular length is about 163 mm.

There are two sacral vertebrae. The length of the tail is not known.

The cervical vertebrae are conspicuous in their degree of elongation, but the dorsals show no such modification. The abrupt decrease, at the level of the first sacral vertebra, of the transverse interzygapophyseal distance is found also in the primitive *Seymouria* and *Captorhinus.*

The mammillary processes of the posterior cervicals and anterior dorsals probably aided in the support of the long neck, and the forwardly inclined spines of the anterior caudals are indicative of a long tail.

The cervical ribs are specialized in their (at least functional) single-headedness. Another noteworthy costal feature is the gradual serial disappearance of the tubercular attachment — the capitular attachment persisting; a similar condition is seen in many mammals.

UC 1708 contains a series of several immature vertebrae, one of which I have figured (Fig. 6, *O*), in which the neural arch and centrum are still widely separated. Though these specimens do not include intercentra, there are large, obvious spaces for such elements. In the mature vertebra, the neurocentral suture is not evident, and the intercentrum is rather small. The larger relative size of the immature intercentrum may reflect a more primitive condition.

Cervical vertebrae (Fig. 5, *A-G*). Unfortunately, none of the more complete skeletons — UC 659, 660, 662 — includes a neck; all conclusions as to the length of the neck and as to the number and serial arrangement of the cervical vertebrae must be drawn from loose, scattered elements and from a number of vertebrae in several small series.

Four of these series have proved valuable in an analysis of the posterior cervicals, and each contains vertebrae from the region of cervical-dorsal transition. Of the two series associated with AMNH 4685 and 4686, one includes eight vertebrac and may be called "AMNH8;" the other contains four vertebrae and is termed "AMNH4." MCZ 2043 contains two series, "MCZ4" and "MCZ7." AMNH8 and MCZ7 are both associated with pectoral girdles, thus allowing the selection of the vertebra here designated as first dorsal to be based on more than the character of the costal articulation alone. The first dorsal, as here defined, is

the most anterior vertebra to show a distinct gap between the areas of capitular and tubercular costal attachment. In MCZ7, the anterior end of the first dorsal lies near the anterior end of the interclavicle, but the position of the rib attached to the third dorsal shows that this vertebral series has been displaced ante-

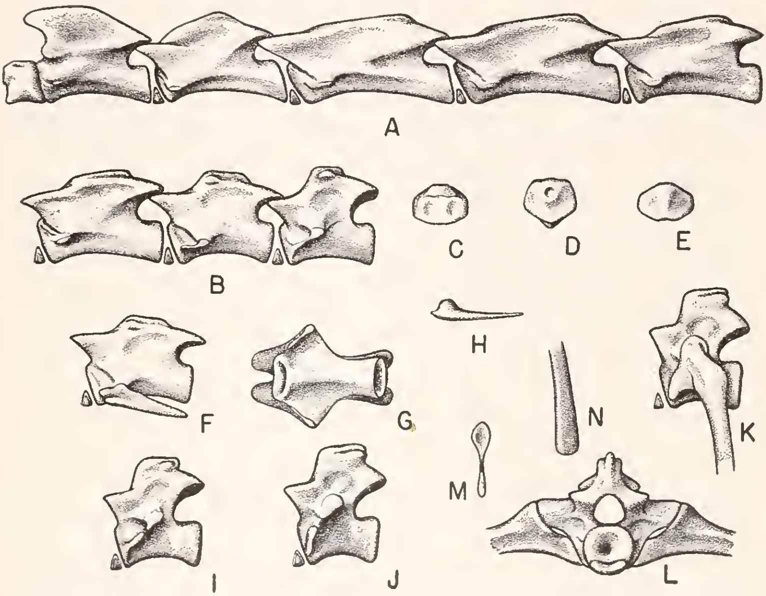

Fig. 5. *A*, First through sixth cervical vertebrae (proatlas, atlantal neural arch, and atlantal intercentrum lacking). *B*, Seventh through ninth cervical vertebrae. *C*, *D*, *E*, Dorsal, anterior, and ventral views of the atlantal centrum. *F*, Eighth cervical vertebrae and rib. *G*, Eighth cervical vertebra, ventral view. *H*, Rib of seventh cervical vertebra. *I*, First dorsal vertebra. *J*. Second dorsal vertebra. *K*, Second dorsal vertebra and proximal portion of rib. *L*, Second dorsal vertebra and proximal portions of ribs, anterior view. *M*, Rib of third dorsal vertebra, proximal view, showing capitulum and tuberculum. *N*, Distal portion of a dorsal rib. All x 4/3.

riorly with respect to the girdle. The condition in AMNH8 seems to indicate the correct relationship; the anterior end of the first dorsal vertebra apparently lay in a common transverse plane with the posterior apex of the diamond-shaped head of the interclavicle.

I have carefully compared the four series and I believe the following tabular correlation to be accurate. There is, of course, some uncertainty as to the numbers assigned the cervical vertebrae.

	C6	C7	C8	C9	D1	D2	D3	D4	D5
AMNH4			1	2	3	4			
AMNH8		1	2	3	4	5	6	7	8
MCZ4				1	2	3	4		
MCZ7	1	2	3	4	5	6	7		

The materials include two atlantal centra (fused with axial intercentra), one attached to a loose MCZ 2043 axis and one attached to the MCZ 1261 skull. Axes are abundant; there are two associated with the American Museum materials, one associated with the Chicago materials, one attached to the MCZ 1261 skull, one attached to the MCZ 2043b skull, and one attached to the above MCZ 2043 atlantal centrum. There is a series of two cervicals in the matrix with the two UC 661 skulls, and there are many loose cervical vertebrae scattered among the American Museum, Harvard and Chicago materials. The picture is greatly confused by many cervical vertebrae quite obviously immature and some not so obviously immature; a series of four fits this first category and a series of three the second, both in UC 1708.

Despite the various degrees of maturity represented in the materials, and despite the absence of any series to fill the gap between the axis and MCZ7, I believe that comparisons among the loose elements permit their placement into reasonable size groupings. I have arranged the vertebrae into a series which shows gradual changes in the build of the neural spines and in the angle of inclination of the end surfaces of the centra. I have, of course, determined that elements judged to be contiguous actually fit one another.

That a gap exists between MCZ7 and the axis is apparent from the presence of specimens of cervical vertebrae longer than any of those in the four correlated series. The variety of lengths among the loose cervical vertebrae indicates a long neck.

In other long-necked reptiles, e.g., *Protorosaurus* and *Macrocnemus*, the third cervical vertebra is longer than the axis but shorter than more posterior vertebrae (based on data from Peyer 1937). This same situation exists in the fairly long-necked lizards *Varanus bengalensis* and *komodoensis* (personal observation,

Harvard specimens). Proceeding on the argument of roughly similar habitus, we may assume the same condition for *Araeoscelis.*

In the reconstruction presented here, three vertebrae have been interpolated between the axis and the first element of the MCZ7 series. The presence of two contiguous elements (C4 and C5 of the restoration) equal in length to one another is based on two such vertebrae found in series in UC 661 and in a submature UC 1708 specimen. The drawing of the axis is a composite of the better specimens of this element. C3 is drawn from a loose American Museum vertebra, C4 and C5 mostly from the UC 661 vertebrae but also from loose Chicago elements. C6 is a composite of the first vertebra of MCZ7 and a corresponding loose American Museum element. C7, C8 and C9 were taken from the four correlated series. There are additional elements, loose or in series, corresponding with the ones selected for the figures.

The weighted average lengths of the centra are (in mm.):

C2	10.6	C6	13.0
C3	12.5	C7	12.0
C4	15.7	C8	10.5
C5	15.7	C9	9.5

Adding the length (4.3 mm.) of the fused atlantal centrum and axial intercentrum, the cervical series is about 103.8 mm. long.

It cannot be overemphasized that the above analysis is without any claim to certainty. More and better materials are needed, but we can be sure that *Araeoscelis* had a long neck.

The proatlas and atlantal intercentrum are not known. The atlantal neural arch is known only from very fragmentary remains attached to the MCZ 2043b skull; these fragments indicate, however, that each demi-arch possessed a posteriorly directed spine which projected for a short distance past the point of articulation with the axis.

The atlantal centrum is indistinguishably fused with the axial intercentrum. The dorsal surface of the resultant composite element contains two small, depressed facets for articulation with the pedicels of the atlantal neural arch. The ventral portion of the anterior surface is recessed to form a large, crescent facet for the atlantal intercentrum. Dorsal to this facet, the anterior surface bears a forward projection, carrying a small notochordal pit,

for articulation with the occipital condyle. A broad, longitudinal ridge lies along the ventral surface. There is no manifest costal facet.

The axis has a neural spine which is anteriorly produced to overhang the posterior half of the "odontoid." Near its anterior edge on each side, the neural arch bears a facet, facing as much laterally as dorsally, for articulation with the atlantal neural arch. A groove for the spinal nerve passes ventrally and posteriorly to terminate shortly behind the anterior surface of the centrum on a level with the notochordal canal. Directly behind the intervertebral groove, at a point buttressed by anteriorly convergent ridges from the neural arch and centrum, lies a very small costal facet. A sharp, longitudinal ridge passes along the ventral surface of the centrum; younger specimens have light accessory ridges.

From the axis posteriorward, the cervical vertebrae show an increase in elongation which reaches its maximum at C4 and C5 (using the working hypothesis for the number of cervicals as presented here). Beginning with C6, the succeeding cervicals show a posteriorward decline in length. The posterior surfaces of the centra of the anterior cervicals are inclined at an angle of about 10° with the vertical. Beginning with C6, the angle of inclination decreases to reach about 0° in C8 and C9. (The dorsals show a slight angle, but in the opposite direction.) Small, gently crescent intercentra are present throughout the cervical series. The dorsal edges of the spines of the more anterior cervicals are somewhat anteriorly sloped; this is especially obvious in C2. This slope becomes less pronounced posteriorly; by C8, the dorsal edge of the spine is completely horizontal. Posterior to the axis, all neural arches show signs of lateral excavation, but the fossa so formed does not become really conspicuous until C9. A mammillary process appears along each side of the neural spine in C8; in C8 this process occurs fairly far anteriorly, in C9 it lies about midway along the length of the spine, and by D1 it has passed to a point near the spine's posterior end. The mammillary processes probably helped support the neck by providing places of attachment for strong intervertebral muscles or ligaments.

The members of each pair of zygapophyses are not widely separated from one another. The prezygapophyses face somewhat medially as well as dorsally, the postzygapophyses somewhat lat-

erally as well as ventrally; their planes are tilted at an angle of 10° or more with the horizontal. The centrum of each cervical vertebra bears a median, longitudinal keel on its ventral surface.

Beginning with the axis, each cervical vertebra carries a costal facet at the anterior end of a ridge running along the side of the centrum. In the anterior cervicals these facets lie rather close to the body of the vertebra, but, posteriorly, they come to extend further laterally so that, by C9, the costal facet lies along the ventral margin of the anterolateral surface of a prominent lateral process. Directly dorsal to its rib-carrying margin, this lateral process is impressed by the lateral extension of the groove for the intervertebral nerve. While the costal articulatory surface of C7 is still rather small, that of C8 is considerably elongate. In the step from C8 to C9, there occurs an abrupt shift in the orientation of the facet; while the axis of the elongate costal facet of C8 is placed almost horizontally, that of C9 meets the horizontal at an angle of about 40°. Though the costal facets of both C8 and C9 show a marked constriction between what may be correctly called the capitular and tubercular areas of attachment, there is still no distinct gap between the two areas. The capitular area of the costal facet of C9, but not of C8, is confluent with the rugose anterior rim of the centrum.

Dorsal vertebrae (Figs. 5, *I-L;* 6, *A-F*, *H*). The skeletons of UC 659, 660 and 662 were prepared from the ventral surface by Williston and display almost complete, articulated sets of dorsal vertebrae. UC 659 has permitted me to determine the serial position of the most anterior dorsal vertebra that lacks a diapophysis. These three sets have also allowed a very close estimate of the number of dorsal vertebrae. The large quantity of other dorsal vertebrae at hand — many loose, but a good number in various series — has enabled me to analyze the serial changes in vertebral structure and costal articulation without the necessity of time-consuming further preparation of the three Chicago sets. This is fortunate since Williston's specimens are embedded in a particularly refractive matrix and, as I have learned from my experience with the other Chicago materials and with the American Museum and Harvard materials, crucial points of transition, such as the serial loss of the posteriorly very small and delicate diapophysis, are best observed in vertebrae removed from a soft matrix or naturally cleaned by weathering. There is also the

unhappy fact that, except for those regions for which there are completely adequate loose series, the costal articulatory surfaces of many of the vertebrae in UC 659, 660 and 662 have not been left in good repair by the preparation and museum residence they have already undergone.

There is a large quantity of loose dorsal vertebrae with the Chicago, American Museum and Harvard collections. Many occur in small series of two or three, but there are also two chains of seven apiece. There are useful series preserved in attachment with both girdles.

Both a Harvard and a Chicago series demonstrate that the anterior face of the second vertebra in front of the sacrum lay nearly in a common transverse plane with the anterior rim of the pubis. Both an American Museum and a Harvard series demonstrate that the mid-point of the glenoid cavity lay nearly in a common transverse plane with the articulation between D2 and D3. While the anterior rim of the pubis is quite evident in UC 662, this specimen contains no remains of the shoulder girdle. However, UC 659 and 660 not only show the anterior rim of the pubis but also (the first by the position of a fairly good scapulocoracoid with an obvious glenoid facet and the second by the position of the head of a humerus) permit the determination of the serial location of the joint between D2 and D3. Counting the vertebrae in each set — pacing off the few small gaps with caliper steps equal in length to the average dorsal — there are eighteen vertebrae between the middle of the glenoid facet and the anterior rim of the pubis. Adding D1, D2 and the last two presacrals, we arrive at the number of dorsal vertebrae: twenty-two. This figure is not far different from Williston's (1914, p. 380) estimate of nineteen or twenty.

The mature dorsal vertebra has an average length of 8 mm., giving a total length of about 176 mm. for the dorsal series. (Since the intercentra are sandwiched into ventral angles between opposing central surfaces, they need not be considered.) Allowing for the fact that the mid-point of the acetabular cavity lies some 3 mm. behind the last presacral vertebra, and subtracting 16 mm. for the combined lengths of D1 and D2, the glenoacetabular length of *Araeoscelis* is about 163 mm. This calculated length is just slightly greater than that measured along the curves of the UC 659 and 660 series, but this was to be ex-

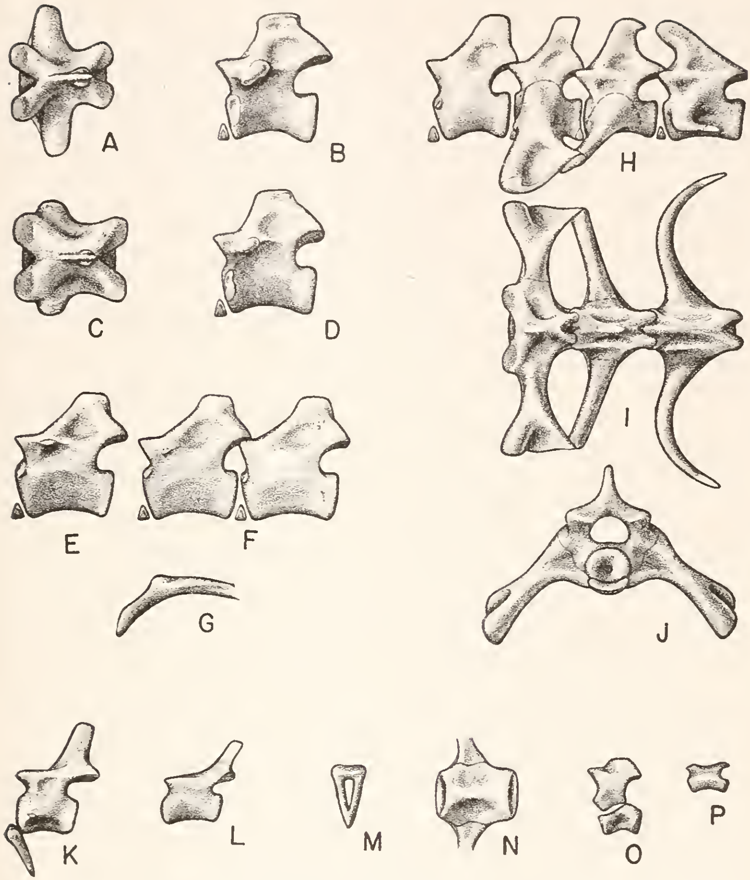

Fig. 6. *A,* Second dorsal vertebra, dorsal view. *B,* Fifth dorsal vertebra. *C,* Fifth dorsal vertebra, dorsal view. *D,* A mid-dorsal vertebra. *E,* A mid-dorsal vertebra from a position farther posterior than that of "*D.*" *F,* Sixth, fifth vertebrae before sacrum. *G,* proximal portion of a mid-dorsal rib. *H,* Last lumbar, sacral, and first caudal vertebrae and sacral and first caudal ribs. *I,* Sacral and first caudal vertebrae and ribs, dorsal view. *J,* First sacral vertebra and ribs, anterior view. *K,* A caudal vertebra and chevron. *L,* A caudal vertebra from a position farther posterior than that of "*K.*" *M,* A chevron, anterior view. *N,* A caudal vertebra and proximal portions of ribs, ventral view. *O,* An immature vertebra. *P,* A posterior caudal vertebra. All x 4/3.

pected, since, judging from the sizes of their limb bones, these specimens are "subadult."

The centra of the cervical vertebrae show a tendency toward a pinched waist accompanied by a longitudinal ventral arch; as a result of shorter length, this condition becomes more pronounced in the dorsals. The dorsals retain the ventral keel of the cervicals, but it becomes less prominent.

The neural arches of all the dorsal vertebrae are excavated by conspicuous lateral fossae. The height of the neural spine, which undergoes a gradual increase in the posterior cervical region, continues to increase through the first few dorsals and levels off at about D5. (Several scattered dorsals of larger than average individuals have relatively longer spines, but there are hardly enough specimens for any allometric study.) The spines of D1 and D2 bear short, backwardly directed extensions, but these fade away to be nonexistent by D5. The mammillary process, alongside the posterior part of the spine, remains well developed through D5 and persists on into the mid-dorsals to slowly vanish; it is not present on the posterior dorsals. The zygapophyseal planes are tilted at an angle of 20° or more with the horizontal.

Small intercentra are present throughout the dorsal series.

D1 bears a heavy lateral process which has roughly the shape of a three-sided pyramid with anterodorsal, anteroventral and posterior edges. The costal surface, with a distinct gap between parapophyseal and diapophyseal areas, lies along the anteroventral edge with the diapophyseal facet spreading onto the apex. The parapophyseal facet is confluent with the anterior rim of the centrum. As in C9, the anterior face of the pyramid bears the lateral extension of the groove for the intervertebral nerve. While the axis of the costal surface of C9 meets the horizontal at about 40°, that of D1 is inclined at about 50°.

In D2, the gap between parapophyseal and diapophyseal facets becomes more pronounced; the first remains close to the centrum while the diapophysis attains its maximal lateral extension. From this vertebra posteriorly, the transverse diapophyseal process becomes gradually shortened. The axis of the costal surface is sharply pitched at an angle of about 65°.

By D5, the parapophysis and diapophysis are completely separate entities. The parapophysis is a vertical ellipse near the anterior margin of the centrum. The diapophysis projects lat-

erally from the side of the anterior portion of the neural arch to end in an oval-shaped facet whose axis is inclined at about 40° with the horizontal. The diapophysis of D5 does not extend nearly as far laterally as does that of D2.

Passing posteriorly, the axis of the diapophyseal facet gradually comes to lie horizontally; the diapophysis decreases in size, becomes very small, and finally disappears altogether. This serial loss is seen in UC 659 and especially clearly in a UC 1708 and in an American Museum series. UC 659 shows that the fifth vertebra in front of the sacrum is the first to lack a diapophysis. The surface of the parapophyseal facet undergoes reduction from below upward, i.e., its ventral border moves dorsally, and, by the vertebral level at which the diapophysis drops out, the parapophysis has been reduced to a small nubbin just anterior to the base of the prezygapophyseal buttress. The parapophysis does not drop out, however, but persists to the end of the dorsal series, even onto the last presacral.

Cervical and dorsal ribs (Figs. 5, *F, H, K-N;* 6, *G*). Only a very limited number of presacral ribs have been preserved, but these represent the conditions at various levels of the vertebral column and, together with the costal surfaces of the vertebrae, give us a fairly good picture of the mode of costal articulation and its serial modification. It will be convenient, below, to refer to the series "AMNH8, MCZ4 and MCZ7," described under the section on cervical vertebrae.

Of cervical ribs, there are: one articulated with a loose MCZ 2043 mid-cervical vertebra (probably C4 or C5), one articulated with a C7 (in MCZ7), one articulated with a C8 (in MCZ7), one associated with a C8 (in AMNH8), one associated with a loose MCZ 2043 centrum (probably C8), and two articulated with C9's (in AMNH8 and MCZ7). The best of the lot are the C8 specimens.

Dorsal ribs are represented by proximal portions articulated, or nearly articulated, with D1 (in MCZ4), D2, D3 (in both AMNH8 and MCZ7), with the third element in a series of three mid-dorsal vertebrae among the American Museum materials, and with a posterior dorsal vertebra in UC 1708. The greater parts of the shafts of several dorsal ribs lie pressed against the internal surface of a pectoral girdle with the MCZ 2043 materials. UC 1708 includes an excellent proximal portion of a rib which

is very probably from D2, several distal parts of shafts associated with a series of seven mid-dorsal vertebrae, and other, scattered bits of ribs.

The only mid-cervical rib known is a proximal fragment attached to the centrum's costal facet. The rib's articular portion, whose limits can be readily made out, is not nearly large enough to have made contact with the small intercentrum too. The absence of any patent neurocentral suture makes it impossible to be sure that the costal facet alongside the centrum is not really attached to a downgrowth of the neural arch, but, in the absence of any evidence to the contrary, it is reasonable to call the articulation of the mid-cervical rib a central one. The rib tapers rapidly into a thin shaft which apparently lay parallel to the long axis of the centrum. The length of the rib cannot be determined.

The rib of C7 bears a head which juts dorsally from the almost horizontal shaft to articulate with the costal facet of the centrum. There is a short, forwardly-directed spine anterior and ventral to the head. The shaft seems not to have extended posteriorly past the centrum.

The costal surface of C8 is constricted between capitular and tubercular areas. The rib, too, shows this division. Its dorsal margin is quite heavy and supports a fairly expanded tubercular facet. The ventral margin is not as thick as the dorsal, but this is correlated with the restricted area of the tubercular articulation as opposed to the elongate capitular articulation. As with C7, the rib of C8 has an anteriorly-directed spine — possibly for the insertion of a M. levator costae. Not far distal to the tubercular articulation, the dorsal margin is gently flared, probably for the insertion of ilio-costal muscles. The rib of C8, subequal in length to its vertebra, was directed posteriorly, somewhat ventrally, and somewhat laterally.

What with the division of its articular surface into capitular and tubercular areas, and in view of the completion of this division in succeeding ribs, the rib of C8 must be looked upon as essentially double-headed (or holocephalous in the sense of Williston 1925, p. 113) rather than as strictly single-headed. Seeing the manner in which the single costal facet of the mid-cervical vertebrae becomes divided into two areas in the posterior cervicals and becomes split into two distinct processes in the dorsals, we might extrapolate to consider all the cervical ribs as holoce-

phalous in the sense of Williston. Their functional single-headedness is probably correlated with the reduction of the intercentra and the elongation of the neck — with its tendency to direct the cervical ribs along an anteroposterior axis.

To have ribs on all the cervical vertebrae is, of course, the primitive condition. It is not possible, however, to determine whether or not this was the case in *Araeoscelis*. The presence of costal facets is not necessarily proof of the presence of osseous ribs but may denote ligamentous attachment (cf. Camp 1923, p. 360).

The only known specimen of C9's rib is poorly preserved. Enough can be made of the rib of D1 to see that the prominent anterior spine, as found on the rib of C8, is not present at this vertebral level.

The capitulum and tuberculum are discrete entities on the rib of D2. The medial end of the rib's thick dorsal margin flares abruptly to form the rim of a shallowly concave tubercular facet which articulates with the laterally produced diapophysis. The neck extends medially and ventrally past the tuberculum and ends in a vertically elongate capitular facet which articulates with the parapophysis not far from the main body of the centrum. The articular surfaces are so placed that the rib is directed not only laterally, but somewhat posteriorly too. Shortly distal to the tuberculum, the dorsal margin of the rib bears a gently swollen, anteriorly-directed prominence, probably for a levator costae muscle. At about this same level, the dorsal margin flares posteriorly into a thin triangle which presumably served for the insertion of ilio-costal muscles. The shaft is flattened in a plane diagonal to the long axis of the trunk, with anterolateral and posteromedial surfaces. A wide groove passes along the posteromedial surface. The distal end of the shaft is slightly dilated; there was, presumably, a connection with the sternum via a cartilaginous or ossified sternal rib, but there are no such elements preserved.

The proximal portions of the mid-dorsal ribs are more lightly built than are those of the anterior dorsals. The rib retains its thick dorsal margin and the prominence for the M. levator costae is still visible. There is no special expansion for the ilio-costal muscles.

UC 1708 contains two small ribs associated with a posterior

dorsal vertebra. These ribs appear to be single-headed, but it is not possible to determine whether or not the associated vertebra possessed a diapophysis. It is conceivable that the osseous tuberculum dropped out — to be replaced by a ligament — at a vertebral level anterior to that at which the diapophysis was lost. It is further conceivable that the parapophyses of the most posterior dorsal vertebrae received ligamentous ''ribs'' rather than ossified elements.

Sacrum (Fig. 6, *H-J*). There are two sacral vertebrae. The Chicago materials include a sacrum of which the two vertebrae and the two left ribs have been preserved in association with the left ischium and the last presacral vertebra. MCZ 1259 includes the distal half of a right sacral rib in association with fragments of a pubis and a presacral vertebra. There is a first and a second sacral vertebra in series in MCZ 1262. MCZ 2043 contains a sacrum, in association with a pelvis, two presacral and five caudal vertebrae, which lacks only the distal half of the left first-sacral rib. MCZ 2043 also includes two loose first-sacral vertebrae and distal portions of three first-sacral ribs preserved with three lateral halves of pelves.

The first sacral vertebra is easily identified because of its location at the vertebral level of an abrupt change in transverse interzygapophyseal distance. The two prezygapophyses of the first sacral are set apart from one another at the same distance that those of the dorsals are, but the two postzygapophyses are separated by less than half this distance. The members of each pair of zygapophyses of the second sacral and of the anterior caudal vertebrae are set apart at a distance equal to that between the postzygapophyses of the first sacral. Posteriorly, of course, this distance decreases along with the overall decrease in size of the caudal vertebrae.

The intercentrum of the second sacral vertebra is fused onto the first sacral vertebra, but the intercentrum of the first sacral itself is free. The height of the neural spine of the first sacral cannot be directly determined from the materials, but, since the last presacral and the second sacral have spines of equal height, that of the first sacral was probably as tall.

The broad, heavy, first sacral rib meets its vertebra, from which it is suturally delimited, in a continuous articulation which begins on the neural arch, passes ventrally and somewhat anteriorly

along the centrum, and ends on the intercentrum. The dorsal and ventral margins of the rib are thicker than the intervening area which is gouged by a broad, shallow groove along the proximal portion of its anterior surface. The rib is directed ventrally and laterally to expand into a fan-shaped distal portion which has a heavy anterior ridge and which thins posteriorly into a dorsally concave plate whose hind edge curls upward at an angle of about 45°. The distal surface of this fan fits into a recess on the medial surface of the iliac blade.

As with the dorsals, the neural arches of both sacrals are laterally excavated, but, with the second sacral, an additional, more ventral fossa appears on the lateral surface just posterior to the prezygapophysis. This fossa persists far into the caudal series but becomes reduced and finally disappears, as does the more dorsal fossa, with the gradual posteriorwards diminution in size of the caudal vertebrae.

The neural spine of the second sacral vertebra is, in absolute measurement, no taller than that of the last presacral, but, because of the lesser height of the second sacral's centrum, its spine is taller relatively. The neural spine of the second sacral bears a small, posteriorly-directed extension near its dorsal end.

An MCZ 1262 specimen shows faint signs of sutural delimitation between the second sacral rib and its vertebra.

The second sacral rib, directed anteriorly at an angle of about 75° with the long axis of the body, bears an oval distal facet which lies close up against the posteroventral edge of the first sacral rib's distal expansion. Thus, both the first and the second sacral ribs enter into direct articulation with the ilium.

The contact between sacrum and ilium is so oriented that the greater part of the first sacral vertebra can be seen lying dorsal to the iliac blade in side view and, taking the ventral edge of the pelvis as the level, the "lumbar" region of the vertebral column meets the horizontal at an angle of about 20°. These conditions are very similar to those found in some other early reptiles, e.g., *Ophiacodon* (cf. Romer and Price 1940, figs. 42 & 43).

Caudal vertebrae and ribs (Fig. 6, *H*, *I*, *K-N*, *P*). There are but a small number of caudal vertebrae among the various groups of materials. None of the skeletons UC 659, 660 and 662 has an attached tail. MCZ 2043 includes a series of the first five caudals articulated with a sacrum and associated with a pelvis, a series

of seven caudal vertebrae — with chevrons — probably from near the middle of the tail, and several loose caudals from the anterior, middle and posterior regions. The Chicago and American Museum materials each include a few scattered, loose caudals from various parts of the tail, and UC 1708 contains a few short series of posterior caudals. MCZ 1262 contains, besides two anterior caudals, a possible fragment of a regenerated tail.

Not nearly enough caudal vertebrae are known to attempt any estimate of their total number. The tail of the reconstruction has a length which may be considered reasonable for a reptile of the size and habitus of *Araeoscelis.*

The neural spine of the first caudal vertebra leans forward at an angle of about 45° with the vertical. The spine of the second caudal leans at about the same angle, but, although this inclination persists, the angle decreases in the immediately succeeding vertebrae; the spine of the fifth caudal seems to have attained near perpendicularity. The forward inclination of the neural spines of the anterior caudals undoubtedly reflects an osseous response to the presence of strong supporting ligaments and muscles for a long tail. Such a response accounts also for the posteriorly-directed extension at the dorsal end of the spine of the second sacral.

The anterior caudals bear long, tapered ribs which pass laterally from their thick bases in gentle, posteriorly concave arcs. The planes of these arcs seem to have been somewhat ventrally inclined. No distal ends of these ribs have been preserved, and we cannot be sure how far posteriorly their recurved tips were prolonged, but the available evidence seems to indicate that they did not extend past their respective vertebrae. The first and second caudals definitely carried such ribs, and, those of the second being nearly equal in size to those of the first, we may expect that the several immediately succeeding vertebrae were similarly equipped except for a posteriorward decrease in the size of the ribs.

Although no patent suture has been found between rib and vertebra in the two most anterior caudals, the clearly demonstrable presence of such sutures in somewhat more posterior caudals among the Harvard materials establishes the described structures as true ribs and not enlarged transverse processes.

The anterior caudals have median, hourglass-shaped longi-

tudinal keels along their ventral surfaces.

The mid-caudals early in the series have short, stubby transverse processes and, relative to their small size, tall neural spines.

The spines of the mid-caudals later in the series follow a general tendency of the whole vertebra to a slight backward inclination. The transverse processes are mere nubbins, and we cannot be sure that they ever bore osseous ribs.

The Harvard series of seven caudal vertebrae shows the gradual reduction and final disappearance of the transverse nubbins and the increase, passing posteriorly, of the backward inclination of the neural spines.

This Harvard series also contains several chevrons. These are obviously outgrowths of intercentra and consist of a crescent, truly intercentral portion and two lateral arms which converge distally to enclose a vertically elongate foramen. A fragment which may be the right half of a long chevron lies near the intercentral space between the second and third caudals and may indicate the anteriormost position of these structures.

In MCZ 1262, there is a gently tapered, tubular fragment of bone, about 18 mm. long, subcircular in cross-section, and covered with prominent, irregularly spaced longitudinal ridges which are more numerous on one side of the specimen than on the other. The lumen has its largest diameter at the wider end of the bone.

It is well known that regeneration of the caudal column in lizards is accomplished by the posteriorward growth of a cartilaginous rod; no new vertebrae are formed. Personal dissection of the regenerated tail of a specimen of *Iguana iguana* has revealed certain strongly suggestive points of similarity to the MCZ 1262 specimen. Both the fossil fragment and the lizard's cartilaginous rod bear irregular, longitudinal ridges, though the ridges of the fossil are more pronounced. Both are perforated by a longitudinal canal, though that of *Iguana* has a smaller lumen. In *Iguana,* the canal carries the spinal cord.

Price (1940) has described a tail-break mechanism in *Captorhinus.* Considering that *Araeoscelis*, in its sternum, shows a tendency toward ossification of normally cartilaginous structures, it is not inconceivable that parts of any regenerated caudal column might have been ossified also. It may be that the described fragment is part of a regenerated tail (See Pl. 2).

Comparison with Previous Interpretations of the Vertebrae and Ribs

Williston originally (1910) mistook the elongate cervical vertebrae of *Araeoscelis gracilis* for caudals, and Case (1911) made the same mistake with the cervicals of *A. casei*. Broom (1913) corrected their error.

The last four elements in Broom's (1913, fig. 2) sketch of several cervical vertebrae are the members of the series AMNH4. Broom's caption shows that we agree in the designation of D1, but that we differ in the arrangement of C3, C4 and C5. Broom stated that no manifest axis was present in the American Museum collection; I find there are two.

Williston (1914) was not able to determine the number of cervicals but set seven as the lower limit. He estimated the number of dorsals to be nineteen or twenty.

Williston gave more or less detailed sketches of a number of vertebrae. These figures are, for the most part, fairly accurate. Better materials indicate certain minor inaccuracies. The spine of the axis available to Williston was anteriorly incomplete, preventing study of the prominent anterior extension. The condition of the Chicago specimens was such that Williston did not see the full height of the spines of the dorsal vertebrae. The badly crushed Chicago sacrum prevented observation of the abrupt decrease in transverse interzygapophyseal distance.

Williston (p. 393) noted the ". . . loss of the diapophysis, which actually occurs in the lumbar region. . . ." With his statement, "The ribs of the neck and lumbar region are single-headed in the strictest sense, not holocephalous. . . . ," I agree with respect to the lumbar region, but, as regards the neck, he was certainly wrong about the posterior cervicals and probably wrong about the anterior cervicals.

PECTORAL GIRDLE

(Fig. 7)

The shoulder girdle is known from fragments with the UC 660 skeleton, from a nearly complete scapulocoracoid associated with the Chicago materials, from parts of coracoids and an interclavicle found with AMNH 4686, from parts of scapula and

coracoids with MCZ 1262, and from several specimens each of scapula, coracoids, clavicle and interclavicle with the MCZ 2043 materials. MCZ 2043 also includes a good part of an ossified sternum.

The dermal elements clavicle and interclavicle are definitely present. No cleithrum has been found (or recognized), but the comment of Romer and Price (1940, p. 114), although given with respect to pelycosaurs, might well be heeded here: "The cleithrum is small, readily detached, and if present liable to be mistaken for a cervical rib. In consequence it is infrequently found and hence has been sometimes assumed to have been absent." Of endochondral elements, there are a scapula, an anterior coracoid, and a posterior coracoid. There is an ossified sternum.

The general build of the pectoral girdle is closely similar to that of pelycosaurs.

Clavicle (Fig. 7, *C*). The clavicle has a narrow dorsal process which lies along the anterior border of the scapula. Though this process is not completely represented in the specimens, it probably terminated dorsally near a forward flare — presumably the acromion — of the scapula about midway up the latter bone's front edge.

Ventrally, each clavicle fans into a thin plate which curves medially over the forward portion of the anterior coracoid to lie external to the respective half of the anterior, depressed part of the interclavicle. The material does not permit a definite statement, but, judging from the surface of the interclavicle, it appears probable that the two clavicles met in the mid-line.

Reasoning from the generally pelycosaurian build of the pectoral girdle, and on the basis of measurements of the interclavicle and coracoids, it is most likely that the ventral plates of the clavicles, together with the interclavicle, extended for some short distance anteriorly past the front edge of the scapulocoracoid.

Interclavicle (Fig. 7, *C*). The interclavicle has a flat, diamond-shaped head and a long stem. The anterior half or better of the head is depressed and lies internal to the clavicles. The raised portion of the head extends anteriorly along the mid-line and between the clavicles for only a very short distance, indicating that the medial edges of the two clavicles were very closely approximated — probably contiguous. The interclavicle's stem is roughly a dorsoventrally compressed ellipse in cross-section;

its sides converge to a median ridge which runs longitudinally along its ventral surface. The anterior part of the stem lay on the external surface of the nearly apposed scapulocoracoids. Posteriorly, the stem lay on the external surface of the sternum. The posteriormost portion of the interclavicle is unknown.

Scapulocoracoid (Fig. 7). The scapulocoracoid consists of three elements, a scapula, an anterior coracoid, and a posterior coracoid. The suture between the two coracoids is clearly seen in the better Chicago specimen. This same specimen indicates, by a sutural break, the position of the division between scapula and coracoids; the location of this latter suture is corroborated by a line seen between the same elements on the inner surface of an MCZ 2043 specimen. All three elements enter the glenoid cavity.

The glenoid cavity is screw-shaped, the anterior part facing backward and somewhat upward, the middle part outward, and the posterior part forward, upward and outward. The anterior part of the glenoid facet projects somewhat laterally and is supported by a buttress which passes anteriorly and ventrally to fade into the general external surface of the anterior coracoid. Directly posterior to this buttress and shortly below the glenoid cavity is the coracoid foramen, best seen in ventral view.

The external surface of the scapula is divided into a blade portion and a supraglenoid buttress. In proportion to the size of the whole scapulocoracoid, the blade is not nearly so tall in *Araeoscelis* as it is in pelycosaurs, but there may have been a cartilaginous suprascapula as in lizards — and apparently in pelycosaurs too (Romer and Price 1940). The blade shows none of the dorsal dilation seen in so many pelycosaurs. A forward flare midway up the blade's front edge may represent an acromion. The hind edge of the blade is the anterior border of the supraglenoid buttress. Just anterior to this border, not far dorsal to the glenoid cavity, lies the supraglenoid foramen. The supraglenoid buttress is triangular with its base along the upper border of the glenoid cavity and its apex, not sharply defined, about a quarter way up the hind border of the scapular blade. The triangle is twisted so that its surface near the apex faces posteriorly rather than laterally.

The external surfaces of the scapular blade and anterior coracoid are smoothly confluent. Two MCZ 2043 specimens demon-

strate that the ventromedial borders of the two anterior coracoids must have been very closely approximated. The outline of the anterior coracoid's front edge is not known.

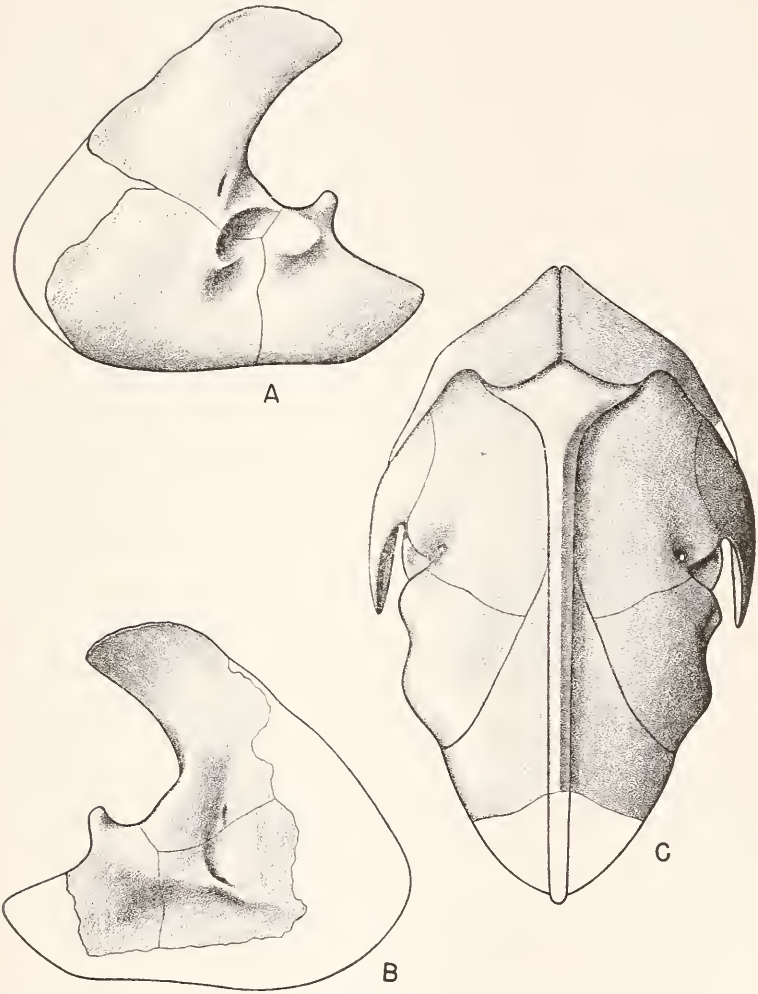

Fig. 7. *A,B,* Lateral and medial views of scapulocoracoid. *C,* Ventral view of pectoral girdle. x 4/3.

Just behind the posterior end of the base of the supraglenoid buttress and directly above the hind part of the glenoid cavity, the posterior coracoid bears a prominent, thumb-like process, presumably for the coracoid head of the triceps muscle.

The medial surface of the pectoral girdle has a large subcoracoscapular fossa which fades anteriorly into the general medial surface of the thin forward part of the scapulocoracoid and which is bounded posteriorly by a thick column of bone formed by the scapula and the hind part of the anterior coracoid. The supraglenoid foramen opens into the upper part of the fossa, the coracoid foramen into the lower part. The coracoids thin rapidly below the level of the glenoid cavity. Except that the posterior coracoid of *Araeoscelis* has a much longer post-glenoid extension, the picture of the medial surface of the scapulocoracoid is very like that seen in pelycosaurs (cf., e.g., *Lupeosaurus,* Romer and Price 1940, pl. 44).

Sternum (Fig. 7, *C*). Though a small posterior coracoid among the MCZ 1262 materials shows a free hind border, a larger coracoid of an MCZ 2043 specimen is in contact with a definite, ossified sternum which, projecting anteriorly to fill in the V-shaped space between the posterior coracoids, is quite similar in position and shape to that seen in *Sphenodon* and many lizards. The interclavicle of this specimen is crushed onto the sternum and it is not possible to determine whether one or two sternal plates were involved. The sternum, as preserved, is posteriorly incomplete. The presence of a sternum in *Araeoscelis* is not at all startling; Romer and Price (1940) assumed it to be present in pelycosaurs but unossified — the usual condition in reptiles. What is unusual about *Araeoscelis* is that its sternum was ossified. Some other early reptiles with ossified sterna are *Lystrosaurus* (Broom 1903), *Youngina* (Broom 1924) and *Tangasaurus* (Piveteau 1926). That of *Araeoscelis* is probably the geologically oldest reptilian sternum to be reported.

Comparison with Previous Interpretations of the Pectoral Girdle

Williston (1914) found no interclavicle or sternum in the specimens available to him, and, indeed, further search has failed to turn up these elements among the Chicago materials.

What Williston (fig. 4*L*) interpreted as a young clavicle is, in reality, a young iliac blade — associated in the matrix with the immature pubis and ischium. I have been unable to recognize any clavicle in the Chicago collection.

The better Chicago scapulocoracoid is almost complete, although broken; Williston's figure (fig. 3*C*) shows it as found. Williston's restoration (fig. 3*D*) is completely erroneous. He assumed (p. 382) that the upper part of the scapulocoracoid was ". . . smoothly broken and turned over the lower. . . ." with the line of breakage acting as hinge-line for the overturning. Such an interpretation forced Williston to the conclusion that there were three distinct, separate glenoid facets — a strange conclusion, considering the quite normal head of the humerus. Williston thought (p. 382) that "There can be no possibility of error in this, since two other fragments, one of which is illustrated in Fig. 3, E, show the same peculiarities." I have no way of recognizing the unfigured fragment alluded to, but I have examined the illustrated fragment, and it is quite obviously a bit of pubis showing the pubic tubercle, the anterior portion of the acetabulum, and the process for the insertion of the ambiens and pubotibialis muscles.

Early in the present study, a plaster cast was made of the overturned upper part of the scapulocoracoid. This cast fits into the lower part of the girdle in such a way that Williston's "upper preglenoid process" is positioned nicely between the "lower preglenoid process" and the "postglenoid facet." When so placed together, these three "processes" described by Williston form one smooth, screw-shaped glenoid facet. The break in the scapulocoracoid is not where Williston thought it to be. The "upper part" is actually an almost complete scapula, broken away from the rest of the girdle and somewhat displaced. A triangle of bone, with anterior base and posterior apex, was lost from that part of the anterior coracoid directly below the scapula. Casts of a *Dimetrodon* scapulocoracoid, broken in a way simulating the fracture in Williston's specimen of *Araeoscelis,* produce a similar picture.

Subsequent preparation of the Harvard materials has revealed several scapulocoracoids, whole in the region of the glenoid cavity, which completely confirm the present interpretation and reconstruction. There is a proximal portion of a humerus articu-

lated with one of these specimens.

Williston did not absolutely commit himself on the question of the number of coracoids. He seems to have considered what we now know to be the suture between anterior and posterior coracoids as the division between coracoid and scapula although he did say (p. 383) that ". . . possibly the lower preglenoid process is on the anterior coracoid, if there be such a bone in this scapula."

Williston unfortunately misled Huene. Taking the figure given by Broom (1913, fig. 3*A*) of the coracoids of *Araeoscelis casei*, Huene (1944a, fig. 5) filled in the rest of the scapulocoracoid to correspond with Williston's reconstruction of that of *A. gracilis*, complete even to the three separate glenoid facets. There is, in the scapulocoracoid described by Williston, a large hole in the anterior coracoid which is obviously a post-mortem defect and not a foramen. Williston figured this hole, and I am certain that he recognized it for what it is, especially since he correctly identified (p. 383) ". . . a notch below the lower preglenoid process. . . ." as part of the coracoid foramen. Huene apparently misunderstood Williston and, misinterpreting a notch — actually part of the coracoid foramen — in Broom's figure of the *A. casei* coracoids, drew a hole to correspond with the hole in the Chicago scapulocoracoid.

Although I can easily see the suture between the coracoids in the Chicago shoulder girdle, I fail to make out the corresponding suture figured by Broom for the American Museum specimen.

ANTERIOR LIMB

(Figs. 8-10)

The overall build of the fore-limb is rather similar to that of lizards. Romer and Price (1940) came to the conclusion that general slimness and elongation of limbs are correlated with absolute body bulk. Heavier muscle attachments necessitate broader limbs, this broadening becoming especially marked in the proximal and distal portions of the humerus. *Mycterosaurus*, with seemingly elongate limbs, has legs actually shorter in proportion to its body size than has *Dimetrodon*, a considerably larger animal. Small reptiles can afford thin limbs; *Ericiolacerta* is a good demonstration of this truth among therapsids. The

similarity between the limbs of *Araeoscelis* and lizards is due to the retention of a basically primitive pattern in both, coupled with modest absolute size and similar habits.

The humerus of *Araeoscelis* is well known from four nearly complete Chicago specimens and a good quantity of excellent fragments from the American Museum, Harvard and Chicago collections. A proximal portion of a humerus in MCZ 1262 is articulated with a scapulocoracoid. The epipodials are not as

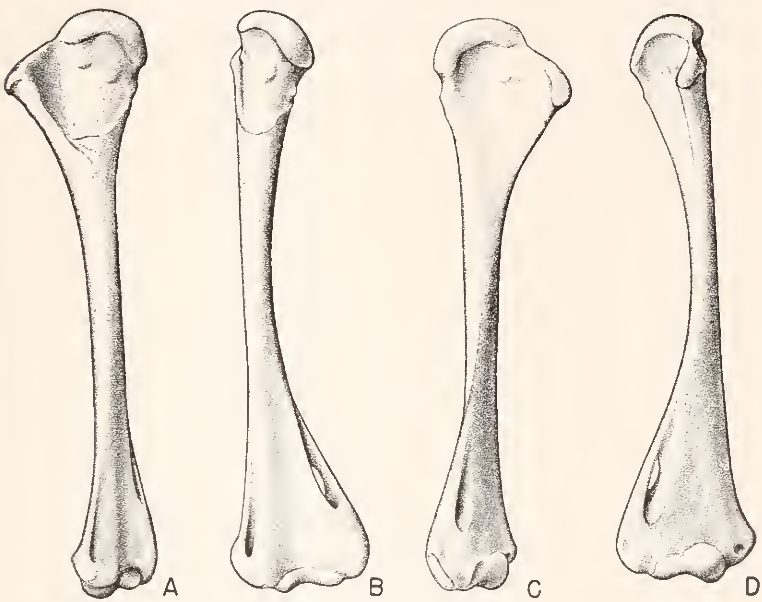

Fig. 8. Humerus. *A,* Proximal dorsal, *B,* distal dorsal, *C,* proximal ventral, and *D,* distal ventral aspects. x 4/3.

well represented. Proximal and distal portions of the radius are present among the loose Chicago, the UC 659, and the MCZ 1262 and 2043 materials. Proximal portions of the ulna have been found in UC 659, MCZ 1262 and 2043.

On the basis of the generally lizard-like habitus of *Araeoscelis,* a rough estimate of the lengths of the epipodials might be attempted. I took two lizards — a specimen of *Varanus griseus* and one of *Iguana iguana* — which approximate *Araeoscelis* in

size, the varanid somewhat smaller, the iguanid somewhat larger. The selection of these specimens was entirely at random; they happened to be in my laboratory. From these animals, I extracted certain ratios of length for comparison with some taken from the materials of *Araeoscelis gracilis*. The humerus/femur ratio for *Araeoscelis* was taken from the most complete humerus and most complete femur and found to be almost identical with the same ratio taken from the associated humerus and femur of UC 660. The tibia/femur ratio was taken from UC 660.

	A. gracilis	*V. griseus*	*I. iguana*
Humerus/Femur	0.89	0.85	0.86
Tibia/Femur	0.97	0.83	0.80
Ulna/Humerus	—	0.91	0.81
Radius/Humerus	—	0.83	0.71

Considering the distant affinities of the animals compared and the relative paucity of available data for *Araeoscelis*, it is hardly worthwhile to measure any further lizards or to work any large series. The humerus/femur ratio is closely similar in the three animals. The tibia/femur ratios show that the posterior propodials and epipodials of *Araeoscelis* more nearly equal one another in length than do the corresponding lizard elements. With this last point in mind, and considering the lizard radius/humerus ratios, I should gauge the radius of *Araeoscelis* to be about 0.90 times as long as its humerus; this is the proportion used in the reconstructions. The missing part of the ulna has been drawn to follow the radius. This was deemed the wiser method since the long olecranon of the *Araeoscelis* ulna makes it difficult to compare this bone with the lizard element.

The ratio arrived at is quite plausible when one compares it with the situation in *Petrolacosaurus* (Peabody 1952) where the anterior epipodials are subequal in length to the humerus.

Humerus (Figs. 8; 11, *A*; Pl. 1). Following the terminology used by Romer and Price (1940), the humeral surface in *Araeoscelis* may be divided into four parts: proximal dorsal, distal dorsal, proximal ventral, and distal ventral. The humerus is a stretched-out version of the primitive tetrahedral type, the proximal and distal planes twisted upon one another at an angle of about 60°. I estimate the epipodials to have met the distal humeral plane at about a 75° angle. Both ectepicondylar and ente-

picondylar foramina are present, the former more distal than the latter. The capitellum is subhemispherical, the trochlea saddle-shaped.

The proximal dorsal surface shows a distinct ridge for the M. deltoideus which passes distally into the line of insertion of the M. latissimus dorsi. There is a hillock for the M. triceps caput

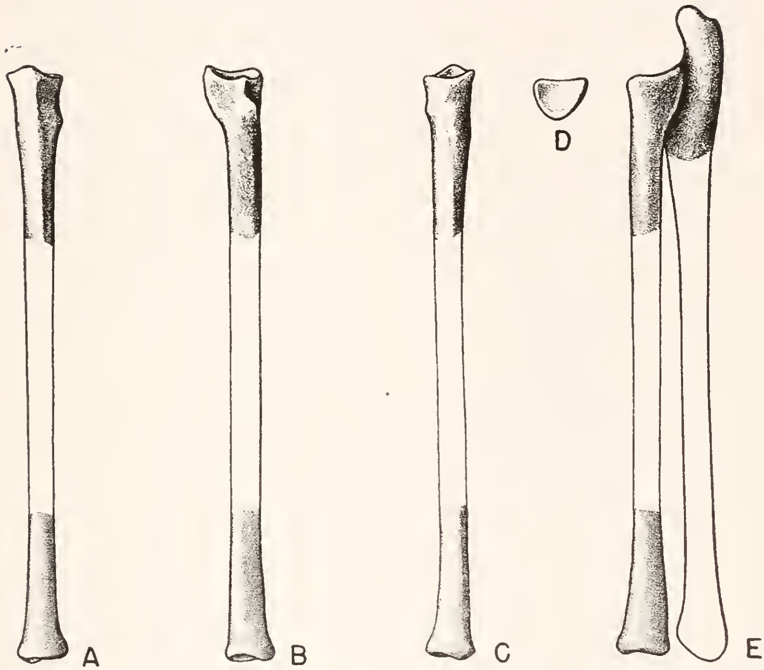

Fig. 9. *A, B, C,* Lateral, postaxial, and medial views of radius. *D,* Humeral surface of radius, proximal view, ulnar edge uppermost. *E,* Radius and ulna, preaxial view. x 4/3.

humeralis lateralis and, shortly posterior and distal to this, one for the M. scapulohumeralis anterior. A small, blunt projection from the posterior border marks the site of insertion of the M. subcoracoscapularis. A sharp ridge indicates the proximal boundary of the fleshy origin of the M. triceps caput humeralis medialis.

The distal dorsal surface shows no particular marks of tendinous muscular attachment. The supinator-extensor crest is somewhat pronounced.

The proximocentral region of the proximal ventral surface bears a distinct projection which probably served as a place of tendinous insertion for the M. coracobrachialis brevis. This is in sharp contrast to the condition in lizards, pelycosaurs and others where this muscle has a broad, fleshy insertion. The area of insertion of the Mm. supracoracoideus and pectoralis on the pectoral crest is best seen in a view of this surface.

The distal openings of the ectepicondylar and entepicondylar foramina are seen on the distal ventral surface. The area of origin of the flexor muscles is fairly well defined and is best seen from a somewhat posterior view of the entepicondyle.

One of the most interesting features of the *Araeoscelis* humerus is the presence of such distinct processes for tendinous muscular attachments. This is especially striking in the case of the M. coracobrachialis brevis, inserted fleshily in, e.g., *Iguana* but tendinously — and at a more proximal and restricted site — in *Araeoscelis.*

The Chicago materials include several immature humeri. In these specimens, the humeral head is lacking, and the ectepicondylar "foramen" is an unbridged groove. It may be that the bony epiphyses arose from secondary centers of ossification — as in lizards. There are no specimens demonstrating any intermediate stage which would indicate the outgrowth of the epiphyses from the diaphyses. A thin section through the distal condyle and adjacent region of an adult humerus has failed to show any sign of separation which might prove the presence of secondary centers, but there would be no reason to expect any such sign in the fully mature individual of a reptile with centers of this sort (cf. Haines 1941). From among the UC 1708 materials, I have prepared an immature humeral diaphysis which has an irregularly shaped, tubular cap of bone at its proximal end in a position where the articular head would develop (See Pl. 1). The cap seems to fit nicely onto the humerus with only a narrow band of matrix separating the two. Extrapolating from Haines' (1941, 1942) papers on the epiphyses of living reptiles, the cap has a build which might be expected of a primitive secondary center. It is embarrassing that there are several small caudal

vertebrae in the same chunk of matrix and that a sagittal section through an isolated centrum of one of these vertebrae would produce an object much like the described cap. The other limb elements do not help decide the matter though, again, epiphyses seem to be either present or absent. It might be significant that an indented line marks off the proximal epiphyseal region from the tibial shaft in almost exactly the same way that the lizard proximal tibial epiphysis is separated from its diaphysis. It may

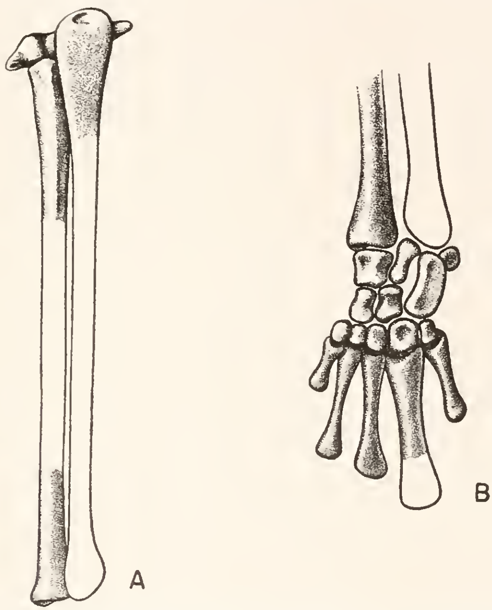

Fig. 10. *A,* Radius, ulna, and distal end of humerus, lateral view. *B,* Carpus, metacarpus, and distal portions of radius and ulna, dorsal view. x 4/3.

be, but is not proven, that *Araeoscelis* included secondary ossification centers as part of its lizard-like habitus. The Jurassic *Sapheosaurus* is the geologically earliest reptile definitely known to possess such centers (Haines 1942).

Radius (Figs. 9, 10). The humeral surface of the radius is cup-shaped to accommodate the capitellum. In proximal view, this surface is a subsemicircle, the straight side applied to the ulna.

The radius has a distinct proximolateral crest to which collateral radial and radio-ulnar ligaments may have been attached (cf. Haines 1946). Proximo-postaxially, there is a protuberance which can only be the bicipital tuberosity.

The lateral and medial surfaces of the shaft have each a longitudinal ridge, that of the lateral surface commencing proximally at the proximolateral crest and that of the medial surface at the bicipital tuberosity. Both these ridges probably indicate the separation of the extensor muscles from the flexors.

The autopodial surface is roughly oval. The narrow, preaxial-medial end of this oval bears a poorly defined styloid process.

Ulna (Figs. 9, *E;* 10, *A*). The ulna has a long olecranon and a concave semilunar notch. The materials do not permit a view of the radial notch. A dimple on the proximal end of the olecranon marks the site of insertion of the M. triceps. This dimple has been observed on two MCZ 1262 ulnae, one of which had to be sacrificed to gain a ventral view of an adherent manus.

Manus (Fig. 10, *B*). MCZ 1262 contains the only specimen of the manus. The carpals are very well displayed. Although no phalanges are attached, the metacarpals are almost complete. As found, the ulnare had been displaced — pivoted around its preaxial border so that its postaxial edge lay directed preaxially on the ventral surface of the carpus. The pisiform had been carried along with the postaxial border of the ulnare and lay preaxial to it on the ventral surface. The intermedium had been rotated about its long axis so that its palmar surface faced dorsally.

The carpus consists of radiale, intermedium, two centralia, ulnare, pisiform and five distal carpalia. The radiale bears a heavy longitudinal ridge on its dorsal surface much as in pelycosaurs. The intermedium extends proximally beyond the common upper limit of radiale and ulnare. One of the most striking features of the *Araeoscelis* carpus is the proximodistal elongation of its preaxial centrale. The preaxial and postaxial centralia are subequal in length; the postaxial one is somewhat wider. The ulnare is the longest element in the carpus, extending from the ulna to the distal carpal row. The ulnare is thickest along its preaxial margin, this thickness most pronounced at the margin's proximal and distal ends. The pisiform is small. The fourth distal tarsal is considerably larger than the others.

Of the metacarpals, the first is the shortest, the fifth second in

length, the second and third subequal with the third slightly the longer, and the fourth the longest and most robust of them all. The fourth metacarpal is distally incomplete in the MCZ 1262 specimen, but an element in UC 659 seems to represent this bone and was used to estimate the length of the restored metacarpal.

Williston (1914, fig. 4) presented figures of several isolated phalanges. Although additional phalanges are known from the Harvard collections, there are not enough to attempt a restoration of the digits. The Harvard phalanges do not differ from those pictured by Williston. There is nothing remarkable about the *Araeoscelis* phalanges; they are of a normal reptilian build, and it would be purposeless to add to Williston's description. I have added a lateral view of a claw (Fig. 14, *L*) although I have no way of knowing whether it is from front or from hind limb. There is no reason to doubt Williston's estimate of 2-3-4-5-3 for the phalangeal formula.

Comparison with Previous Interpretations of the Anterior Limb

Williston's reconstruction (1914, fig. 2) has the planes of the humeral extremities twisted at too great an angle — almost 90° — to one another. A complete humerus in the Chicago collection does show almost a right angle twist, but this specimen consists of five serial fragments, and the angle was exaggerated during the joining of these pieces. Another complete Chicago specimen demonstrates a more modest angle.

Williston did not describe any of the muscular attachments, but his figure does show the tuberosity for insertion of the M. scapulohumeralis anterior.

The Harvard materials have confirmed Williston's conviction that the entepicondylar foramen was bridged over. Broom's figure (see below) gives the same confirmation.

Broom (1913, fig. 3*B*) joined a proximal and a distal portion of a humerus of *Araeoscelis casei* to form a short bone with both extremities in a common plane. Williston (1914, p. 384) criticized Broom's work: "One would not recognize the figure given by Broom of the humerus of *Ophiodeirus* as that of an allied animal even, much less as that of *Araoescelis,* were it not for the statement in the text that the two ends of the specimen, as fig-

ured, did not connect with each other. He thought that little was missing and figures the two ends in the same plane, though an examination of the humerus of *Araeoscelis,* as figured by me, should have convinced him of his error. As a matter of fact, taking as indices the two ends as figured, a slender cylindrical piece of the shaft 12 mm. in length was missing. . . ."

Williston recognized the olecranon of the ulna in UC 659. His descriptions of the distal ends of the ulna and radius are incorrect since they were based upon the distal ends of tibiae and fibulae associated with tarsi which Williston had erroneously identified as carpi.

Williston mistook two tarsi for carpi. His restoration of the carpus (fig. 2*F*) is, therefore, to be disregarded. Due to the incorrect identification on which Williston proceeded, his restoration does not resemble even the tarsus. This matter will be discussed again under the section on the tarsus.

In 1914 Williston gave the phalangeal formula 2-3-4-5-3 as an hypothesis — all that the material allows — but later (1925, p. 195), undoubtedly a *lapsus*, stated it as fact.

PELVIC GIRDLE

(Fig. 11)

UC 659, 660 and 662 present good ventral views of the pubes and ischia. Associated with these finds are a right ischium, with a sacrum, and smaller pelvic scraps. There are more fragments among the UC 1708 materials, including an immature pelvis with all three elements present — separated but closely associated in the matrix. There are parts of all three elements in MCZ 1259. Many good specimens in MCZ 2043 give us an almost complete picture of the pelvis.

The pelvic girdle is of a primitive type, more closely similar to that of ophiacodontid pelycosaurs than to the pelvis of any other group. Ilium, pubis and ischium all enter the acetabulum. The anterior, anterodorsal and posteroventral margins of the acetabular cavity are thick and raised; the cavity is open along its posterodorsal and ventral margins. The pubes and ischia together form the plate-like structure so characteristic of early reptiles. That the ventral elements of the two sides were contiguous along their medial borders is clearly seen in UC 659, 660 and 662.

In ventral view, there is seen a small, diamond-shaped vacuity at the point of intersection of the sagittal and transverse sutures of the puboischiadic plate. As Romer and Price (1940) have pointed out for pelycosaurs, this vacuity does not represent the puboischiadic vacuity of advanced forms; this latter opening is centered in the area of origin of the M. puboischiofemoralis externus. The vacuity in *Araeoscelis* was probably filled with cartilage.

Ilium (Fig. 11). The anterodorsally directed thrust of the hind limb fell upon the ilium, and, accordingly, this element con-

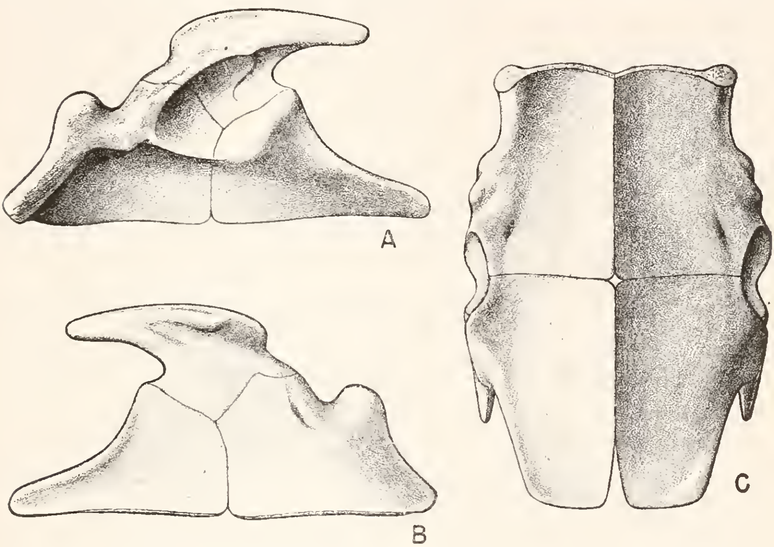

Fig. 11. Pelvis. *A*, Lateral, *B*, medial, and *C*, ventral views. x 4/3.

tributes an anterodorsal buttress to the acetabular facet. The iliac blade shows very little anterior development but is extended for a considerable distance posteriorly past the acetabular region. The centrodorsal region of the medial iliac surface is recessed to receive the sacral ribs.

Pubis (Fig. 11). The pubis contributes the anterior part of the glenoid cavity and makes up the front half of the puboischiadic plate.

The lateral margin of the pubis is formed into a thick, rounded

ridge which passes anteriorly and ventrally from the region of the acetabulum to terminate distally on a level with the pubic symphysis. A short distance anterior to the acetabulum, a prominent, somewhat laterally compressed tubercle — corresponding to the "lateral pubic tubercle" of ophiacodonts (Romer and Price 1940, p. 132) — projects dorsolaterally from this ridge. There is a less pronounced ventral projection from the part of the ridge between tubercle and acetabulum. Romer and Price felt that the lateral pubic tubercle of ophiacodonts served as a place of origin for the Mm. ambiens and pubotibialis. From an inspection of diagrams given by Romer (1922, pl. 44) of the areas of thigh muscle origin in *Dimetrodon* and *Iguana,* I submit that the Mm. ambiens and pubotibialis of *Araeoscelis* were attached to the ventral projection from the pubic ridge rather than to the lateral pubic tubercle. As to the function of the tubercle: The M. puboischiofemoralis internus undoubtedly passed from the medial surface of the pelvis outward under the ilio-pubic ligament and through a notch formed between the lateral pubic tubercle and that portion of the pubis immediately anterior to the acetabulum. I suggest that the lateral pubic tubercle served to raise the anteroventral end of the ilio-pubic ligament and that its presence is to be correlated with the absence of a good anterior extension of the iliac blade. When the pelves of ophiacodonts are compared with those of sphenacodontids and edaphosaurs (cf. Romer and Price 1940, figs. 25-28), the latter two groups are seen to differ from the first by: 1) the lack of a lateral pubic tubercle and 2) the presence of a good anterior extension of the iliac blade. This extension permits the ilio-pubic ligament, even in the absence of a raised anteroventral anchoring-point, to ride high above the course of the M. puboischiofemoralis internus. The anterior extension of the iliac blade is, of course, concerned with more profound changes in the placement of dorsal limb musculature; indirectly then, such changes rendered the lateral pubic tubercle unnecessary.

The external opening of the obturator foramen, best seen in ventral view, lies shortly medial and posterior to the pubic ridge's ventral projection. The foramen passes dorsally through the pubis and opens internally above and behind the presumed major area of origin of the M. puboischiofemoralis internus.

A transverse section through the middle of the pubes would

show each pubis to be gently convex in a dorsomedial direction and would demonstrate a median trough formed by the contiguous elements.

Ischium (Fig. 11). The ischium contributes the heavily buttressed posterior portion of the acetabular facet and thins rapidly ventrally and posteriorly. Though the ventromedial edges of the two ischia are in contact for most of their lengths, there is a short, V-shaped space separating them posteriorly.

Comparison with Previous Interpretations Of The Pelvic Girdle

Williston's (1914, fig. 4*V*) restoration of the pelvis has the ilium and ischium essentially correct; my interpretation differs in small details, e.g., a more extensive ischiadic contribution to the acetabular facet.

While Williston noted the thickening of the lateral pubic margin, his sketch did not sufficiently emphasize this feature. His materials were not good enough to enable him to recognize the ventral projection to which I feel the Mm. pubotibialis and ambiens were attached. His restoration lacks the lateral pubic tubercle and the obturator foramen; both were available to him in UC 662 and the second in UC 660 too. The lack of the foramen is especially puzzling since it is clearly shown in two of Williston's drawings (figs. 1*A* and 2*A*) of the materials as preserved.

Broom's (1913) description of *Araeoscelis* (*Ophiodeirus* of Broom) *casei* suffers greatly from the fact that one is often unsure whether, in a particular sentence, Broom was speaking of *A. casei* or of *Bolosaurus striatus*. After discussing parts of the postcranial anatomy of *A. casei*, Broom launched directly into the description of a pelvis and gave a figure (fig. 4). His figure of this pelvis is labeled "*Bolosaurus striatus*" and is probably truly of that animal. This is especially probable when we consider that there is no resemblance between the figure given by Broom and the pelvic girdle of *Araeoscelis*. Broom's seeming carelessness is undoubtedly accounted for by the fact that he considered *A. casei* and *B. striatus* to be closely related. That Williston found Broom's paper difficult reading is evidenced by one of Williston's opening phrases (1914, p. 387): "Broom compares the pelvis of *Ophiodeirus,* or his so-called *Bolosaurus*. . . ."

POSTERIOR LIMB

(Figs. 12-14)

The general build of the posterior limb is, like the anterior limb and for probably the same reasons, rather lizard-like. Again, such similarity is most likely due to a basically primitive pattern modified by light build and lizard-like habits. The femur and epipodials are almost completely known. The tarsus and most of the metapodium are well known, but phalangeal information is extremely limited. The propodium and epipodium are subequal in length. The epipodium is rather distinct in the pronounced anterior concavity of the tibial shaft.

Femur (Figs. 12; 13, *A*). The femur is known from UC 659, 660, 662, an associated complete, loose specimen, and associated mature and immature parts. UC 1708 contains two immature specimens, one associated with a pelvis. MCZ 1259 contains proximal fragments. MCZ 2043 includes one complete femur, one proximal portion articulated with a pelvis, and a number of excellent fragments.

In pre- or postaxial view, the femur is sigmoidal in shape, the proximal part of the shaft dorsally concave, the distal part dorsally convex.

Shortly distal to the head, there begins a prominent anterior crest which fades distally onto the ventral surface of the shaft to form a linea aspera for the insertion of the adductor muscles. The crest's proximal end is produced into an internal trochanter (cf. Romer 1924) for the insertion of a tendon of the M. puboischiofemoralis externus. There is no manifest fourth trochanter.

On the postaxial border, just distal to the head, there is a conspicuous tuberosity whose direction marks it as the probable site of insertion of the M. ischiotrochantericus.

Two low ridges, one beginning on the preaxial surface and one on the postaxial surface, pass proximally to converge — but remain widely separated — on the shaft's dorsal surface. Undoubtedly, the fleshy origin of the M. femorotibialis crept proximally between these two ridges to separate the two major areas of insertion of the M. puboischiofemoralis internus, the one anterior to the preaxial ridge, the other posterior to the postaxial ridge.

The distal dorsal surface of the femur is indented by an inter-

condylar fossa through which slid the tendon of the quadriceps muscle.

The proximal ventral surface is occupied by the intertrochanteric fossa which must have received the fleshy part of the insertion of the M. puboischiofemoralis externus. The insertion of the M. iliofemoralis probably lay immediately distal to the intertrochanteric fossa, bounded by a slight ridge posteriorly and by the proximal beginnings of the linea aspera anteriorly.

The popliteal area is deeply recessed from the general distal ventral surface.

The postaxial portion of the distal end of the femur projects distally between the head of the fibula and the cnemial process of the tibia. The femur is notched by a distinct fibular facet.

Tibia (Figs. 13; 14, *A, G, H*). The Chicago collection contains two nearly complete specimens with UC 659 and 660, a proximal portion with UC 662, and several very good loose fragments including, among others, a distal portion articulated with a pes and two specimens in each of which the proximal parts of the tibia and fibula are in articulation with the distal portion of the femur. MCZ 1259 includes proximal and distal parts; MCZ 1262 contains a proximal part articulated with a fibula; and in MCZ 2043 there are: an almost complete tibia alongside most of a fibula, a second almost complete tibia lacking only the head, and a good number of fragments.

The tibia is immediately distinctive in the conspicuous anterior concavity of its shaft. This curvature is readily seen in several of the more complete specimens; its direction is demonstrated by the mode of tibio-astragalar articulation and is evident from the placement of the fibula in those cases in which the tibia and fibula have been preserved in more or less natural relationship to one another.

The articular surface of the head is roughly a triangle with a convex medial base and an apex which is directed laterally and somewhat postaxially. A broad, indistinct ridge divides this surface into preaxial and postaxial articular areas. The apex supports a large, knob-like cnemial process for the insertion of the quadriceps muscle.

The outline of the articular surface is impressed onto the whole proximal portion of the shaft, giving it a triangular cross-section. Just distal to the articular surface and parallel with

its preaxial side, a distinct groove marks off the proximal epiphysis.

A heavy ridge passes distally from the cnemial process, curves gently in a postaxial direction, and fades into the general surface of the shaft.

A longer, lighter ridge starts below the postaxial corner of the articular triangle, passes distally along the postaxial border of the shaft to curve anteriorly and fade out about one-sixth of the way above the tibia's distal end. This ridge may have afforded the anterior line of attachment for an interosseous ligament.

The astragalar articulatory surface is divided into two parts: 1) a trough-like lateral, somewhat postaxial portion for articulation with the proximolateral tibial ridge of the astragalus, and 2) a medial, somewhat preaxial projection for articulation with the astragalus' distomedial tibial shelf. On the preaxial surface just proximal to this projection, there is a small, rugose area to which an astragalar ligament may have been attached.

The tibio-astragalar joint is a firm, locked one.

Fibula (Figs. 13, *A*; 14, *A*). The fibula is seen almost complete in UC 659 and 660. The loose Chicago materials contain two proximal fragments in articulation with tibiae and femora and two distal pieces in association with pedes. MCZ 1262 and 2043 both include proximal portions of fibulae in association with proximal parts of tibiae, and 2043 contains a nearly complete fibula alongside a tibia.

The fibula is a blade-like bone, with pre- and postaxial "cutting" edges. The preaxial edge is the sharper and probably served as the posterior line of attachment of an interosseous ligament. In lateral view, the proximal portion of the blade is narrow, the distal portion dilated. The fibular shaft shows a general preaxial concavity which is most pronounced distally.

The tibia has no distinct fibular facet; the articulation of the fibula's slightly swollen proximal head was almost entirely femoral with only a minor tibial contact. The head fits into an obvious notch on the femur.

The fibula's distal articular surface is shared almost equally by the astragalus and calcaneum. The distal ends of the tibia and fibula are widely separated.

Pes (Fig. 14). The structure of the tarsus and most of the metatarsals can be readily made out from a relatively extensive

suite of materials. UC 659 has both right and left pedes in plantar exposure at the distal ends of their respective epipodia; the elements are scattered and, of the metatarsals, only proximal parts are present. There are two excellent, loose pedes in Chicago. One has all the tarsal elements and the proximal parts of the second, third and fourth metatarsals. The other has the astragalus, calcaneum, part of the cuboid, and the proximal

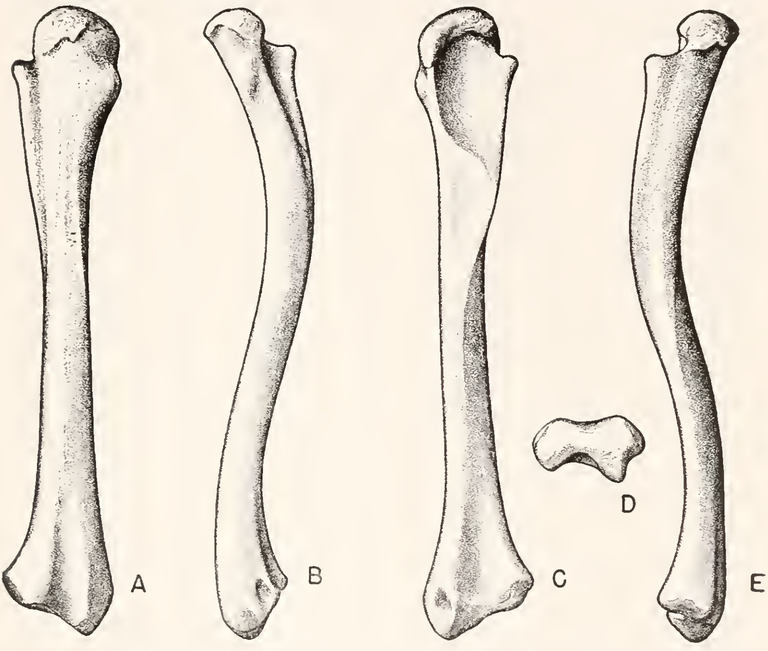

Fig. 12. Femur. *A*, Dorsal, *B*, postaxial, *C*, ventral, and *E*, preaxial views. *D*, Distal end of femur, dorsal surface uppermost. x 4/3.

portions of all five metatarsals. UC 1708 contains astragalus, calcaneum, outlines on the matrix of the other tarsals, and the proximal parts of the second, third and fourth metatarsals. There is a loose fourth metatarsal in Chicago. The American Museum materials include a tarsus which lacks only the first two distal tarsalia. MCZ 1262 contains a free astragalus and free proximal parts of the fourth and fifth metatarsals. MCZ

2043 contains an articulated calcaneum and cuboid and a tarsus complete except for the first two distal tarsalia.

The tarsus consists of astragalus, calcaneum, one centrale conveniently called the navicular, three free distal tarsalia, and an element composed of the fused fourth and fifth distal tarsalia and conveniently called the cuboid. The two most distinctive bones of the *Araeoscelis* tarsus are the astragalus and cuboid. Both these elements are found in the Chicago, American Museum and Harvard collections and offer excellent marks by which the animal may be identified.

The astragalus has a short neck whose proximal end forms half of the tarsal fibular surface. The postaxial border of the astragalus passes vertically from the fibular surface, is interrupted near its distal end by a notch which forms the preaxial part of a foramen for a perforating artery, and is distally confluent with the condyloid structure at the corner of the postaxial and distal borders. The preaxial border slopes preaxially and distally for two-thirds of its length, then makes a right-angle turn to run postaxially and merge with the distal border. The distal border is notched between its preaxial end and the condyloid corner.

The astragalus has two distinct tibial surfaces. The one, which may be called proximolateral, takes up the heavily thickened distal two-thirds of the preaxially sloped portion of the preaxial border. The other, which may be called distomedial, is a shelf, on the medial (plantar) surface, which runs parallel with and shortly distal to the proximolateral tibial surface. As already described, the distal articulatory surface of the tibia is divided into two areas, a lateral trough and a medial projection. The trough fits onto the proximolateral tibial surface of the astragalus, the projection onto the distomedial shelf. The whole makes for a firm, locked joint. Part of the tibia's projection extends medially from the joint and may have afforded an area of origin for short digital flexor muscles.

The medial surface of the astragalus shows a large fossa which leads to the perforating notch.

The condyloid corner of the astragalus articulates with the preaxial end of a trough on the cuboid's proximal surface and is an integral part of the functional ankle joint.

The calcaneum is composed of a heavy preaxial portion, bearing a fibular facet on its proximal end, and a thin, dilated post-

axial plate which is buttressed by a medial, horizontal ridge. The preaxial surface shows two areas for articulation with the astragalus. One area lies proximal to the perforating foramen; the other lies distal to the foramen and is recessed to articulate with the condyloid corner of the astragalus. The supraforaminal portion of the postaxial border of the astragalus overlaps the calcaneum medially; the two elements probably acted as a unit with very little movement between them.

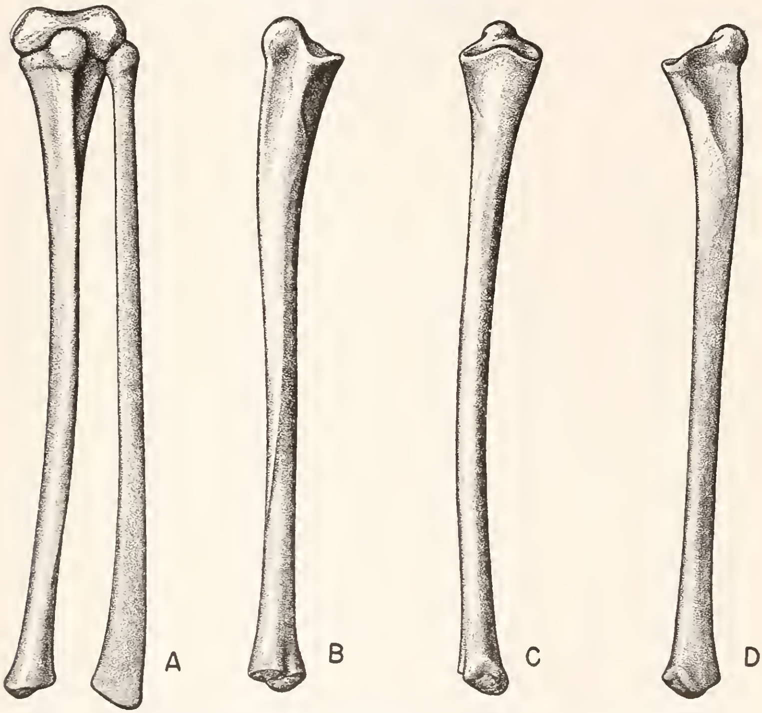

Fig. 13. *A*, Tibia, fibula, and distal end of femur, lateral view. *B, C, D*, Postaxial, medial, and preaxial views of tibia. x 4/3.

The direction of the perforating foramen, as demonstrated by the direction of both the astragalar and calcaneal components, indicates that the artery must have passed from the medial surface distally and outward to the lateral surface. This is the same direction in which the foramen runs in, e.g., pelycosaurs

and *Captorhinus* (person. observ.). This feature may be used as a mark of recognition of the lateral (dorsal) surface as opposed to the medial (plantar) surface.

The distal border of the calcaneum is rounded to be received into the trough on the proximal surface of the cuboid.

The trough of the cuboid is carried onto the proximal surface of the short, broad navicular where it becomes less pronounced.

It is possible that a cartilaginous preaxial centrale was interposed between the astragalus and the first distal tarsal since the latter received very little direct support from the navicular. The second distal tarsal is the smallest. The third distal tarsal bears a short arm which overlaps the second distal tarsal proximally.

The cuboid is a large bone composed of the fourth and fifth distal tarsalia. In dorsal view, the two elements seem to be indistinguishably fused, but the vestigial suture between them can be discerned on the plantar surface. This suture can be easily made out on one UC 659 and two MCZ 2043 cuboids, and it is the line of fracture in the American Museum cuboid where the component elements have been slightly displaced, one from another.

The cuboid overhangs the third distal tarsal proximally. Its tapered postaxial portion is free of calcaneal contact. The area of the plantar surface immediately distal to the calcaneum is recessed from the general surface.

The articular surface for the fourth metatarsal faces somewhat dorsally as well as distally so that the metatarsal (there being probably little or no tarsometatarsal movement) met the cuboid at a fixed, dorsiflexed angle of about 165°.

The cuboid receives the condyloid corner of the astragalus and the distal edge of the calcaneum into its trough-like proximal surface. This mode of articulation, plus the fact of immobility at the tibioastragalar joint, constitute strong evidence that the functional ankle joint was mesotarsal with the axis of movement lying along the boundary between the functionally crural astragalus and calcaneum and the functionally pedal navicular and cuboid.

The mesotarsal articulatory surfaces are not nearly as well developed as they are in, e.g., lizards, and it is doubtful whether any really appreciable degree of dorsiflexion could have taken place. With this in mind, and considering the obtuse angle of

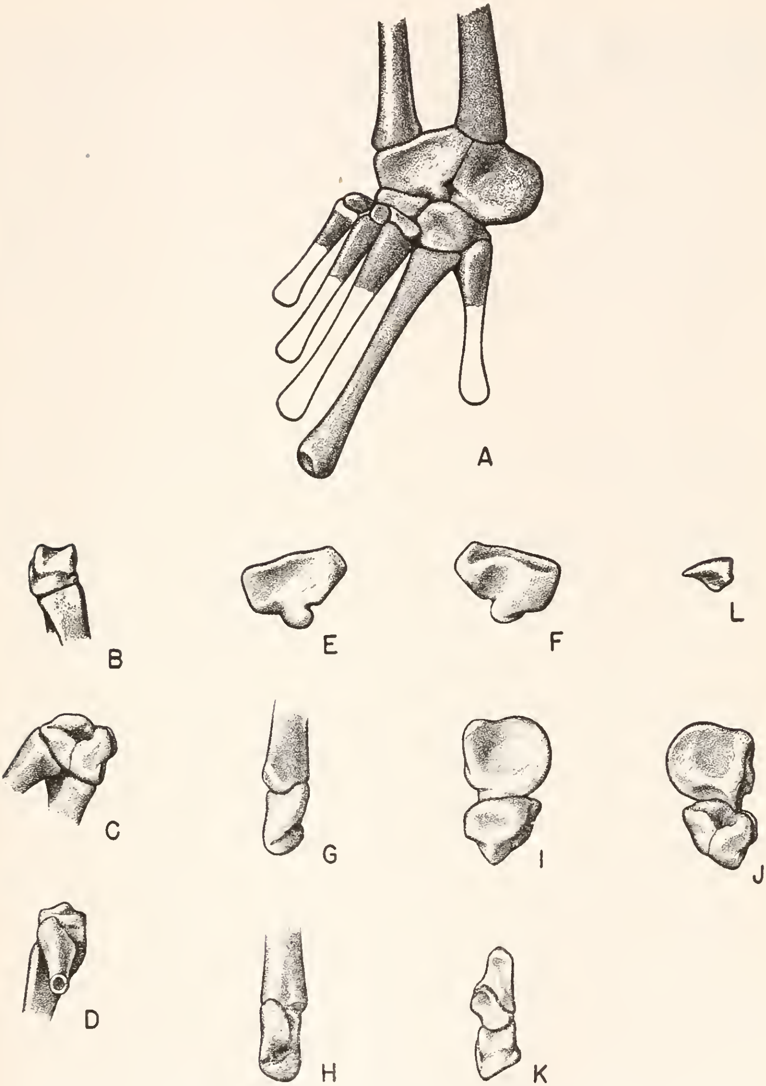

Fig. 14. *A,* Tarsus, metatarsus, and distal portions of tibia and fibula, lateral (dorsal) view. *B, C, D,* Preaxial, plantar, and postaxial views of cuboid, fourth and fifth metatarsals. *E, F,* Lateral (dorsal) and medial (ventral) views of astragalus. *G, H,* Preaxial and postaxial views of astragalus and distal portion of tibia. *I, J, K,* Lateral (dorsal), medial (ventral), and preaxial views of calcaneum and cuboid. *L,* A claw. All x 4/3.

fixed dorsiflexion between cuboid and fourth metatarsal, it seems highly probable that the metatarsals, except for perhaps their distal ends, never touched the ground. Thus, in walking or running, the only elements of the hind feet that regularly touched the ground were the phalanges; *Aracoscelis* walked on its toes. This analysis agrees entirely with conditions seen in many ''araeosceloid'' trackways from the Clear Fork beds. Donald Baird (personal communication 1954), who has studied several of these trackways, is of the opinion that they were made by reptiles whose hind metapodia never touched the ground except for occasional contacts by the metatarsophalangeal pads.

The distal portions of the first, second and third metatarsals are not known, but, judging from the rather long fourth metatarsal and the generally lizard-like habitus of the pes, there was probably a gradual increase in length from the first to fourth metatarsals. The proximal portions of the third and fourth metatarsals are triangular in cross-section, with a narrow dorsal base and a plantar apex; the apex lies preaxially so that the preaxial surface of the metatarsal is set at nearly a right angle to the general plantar plane while the postaxial surface intersects the plane at an angle of about 45°. The fourth metatarsal overlaps the fifth proximally; I cannot detect any overlapping among the other metatarsals.

The fourth metatarsal is the longest and most robust. Its proximal part occurs articulated in UC 1708, the two loose Chicago pedes, and nearly articulated in the American Museum pes. A loose MCZ 1262 proximal portion fits nicely an MCZ 2043 cuboid. There is a complete metatarsal, associated with UC 659, whose proximal portion corresponds in every way with the articulated proximal portions. This metatarsal was used to complete the restoration.

The proximal portion of the fifth metatarsal is known articulated in one of the loose Chicago pedes. This element is completely different from any of the other metapodials, permitting the Chicago fifth metatarsal to be used in the identification of a loose, proximal portion of a fifth metatarsal in the MCZ 1262 collection. This latter specimen fits snugly against the disto-postaxial part of an MCZ 2043 cuboid in such a way that it is divergent from the fourth metatarsal at an angle of about 40°.

The fifth metatarsal is not dorsiflexed as is the fourth; rather, its dorsal surface lies in almost a common plane with the dorsal surface of the cuboid. The fifth digit undoubtedly served as a lateral prop for the hind limb.

As with the manus, there are loose, scattered claws and phalanges similar to those pictured by Williston (1914, fig. 4) but no way of determining whether they are elements of the anterior or of the posterior limb. There are not enough of these elements to attempt any reconstruction of the pedal digits. These bones do not differ from the usual reptilian type of phalanx.

Comparison with Previous Interpretations of the Posterior Limb

Williston (1914) did not discuss any of the muscular attachments, but the two views (dorsal and preaxial) which he gave of the femur show basic agreement with the description of the lines and ridges as presented in the present paper. Williston's materials were not good enough to permit him to recognize the protuberance which I interpret as the place of insertion of the M. ischiotrochantericus.

Williston's restoration of the tibia does not show its pronounced curvature. He was, however, doubtful on this point and said (p. 389): "The tibia [of UC 659] . . . has apparently undergone a slight external curvature, though it is possible that this curvature is natural, and that I have represented the shaft in Fig. 5, *E*, too straight on the lower part." Had the tibia of UC 659 been more fully prepared, he would have seen that the specimen whose distal end he figured as "fibula, distal end" was, in reality, a distal portion of a tibia. The proximal portions of the tibia and fibula are not as closely articulated as Williston (fig. 5*E*) thought them to be.

Williston had five specimens of the tarsus available to him. Two of these are loose and were misidentified by him as carpi. These two may be discussed first.

Only one of these was at all well prepared, and it is obvious from Williston's description (p. 384) that this is the specimen on which he based his reconstruction (fig. 2*F*) of the manus. The astragalus is displaced; subsequent preparation has revealed that the cuboid is broken and that its two fragments lie apart

from one another. This preparation has also exposed the quite distinctive distal end of the tibia and has shown Williston's "radiale" to be a well-formed astragalus.

Williston added, in dotted line, three preaxial elements: a centrale, a distal mesopodial, and a metapodial. There is no evidence for the existence of the first of these. Williston added the other two because he thought the fourth metatarsal to be the fifth. A listing of the correct identities of the elements actually present will suffice.

Williston's identification	*Element of hind foot*
radius, ulna	tibia, fibula
radiale, ulnare	astragalus, calcaneum
intermedium	preaxial part of cuboid
centrale	centrale
second distal carpal	first distal tarsal
third distal carpal	second distal tarsal
fourth distal carpal	third distal tarsal
fifth distal carpal	postaxial part of cuboid
third metacarpal	second metatarsal
fourth metacarpal	third metatarsal
fifth metacarpal	fourth metatarsal

Of the second loose tarsus which he misidentified, Williston wrote (p. 385): "The second specimen includes the epipodial and mesopodial bones and the proximal ends of the first and second metacarpals; the intermedium is not visible, possibly it is lost. There is also much more of the metapodials than in the other specimen, though none is complete." Subsequent preparation has shown this specimen to include the following: almost perfect astragalus and calcaneum, postaxial part of cuboid, and the proximal parts of all five metatarsals — including the distinctive fifth metatarsal lying in its proper position with respect to the others.

Of the three tarsi which Williston identified correctly, two are at the ends of their respective epipodia in UC 659, and one is articulated with a fibula in UC 1708.

Williston figured (fig. 1) both UC 659 tarsi in a general sketch of the UC 659 skeleton but chose the right one for a detailed figure (fig. 5*J*). This was an unfortunate choice because it is the left tarsus which shows an almost perfect cuboid — in plantar view. The right tarsus is poorly preserved. Williston's drawing

of the astragalus is inaccurate, but the identification is correct. I suspect that what he labeled as the first distal tarsal is, in reality, the navicular, displaced in restoration. It is difficult to correlate the other elements in Williston's figure with the bones actually present, but the specimen seems to include the third distal tarsal, part of the cuboid, and the proximal parts of the second, third and fourth metatarsals.

It is to Williston's credit that he recognized, from his observation of UC 659, that (p. 389): "Its [the astragalus'] articulation with the tibia seems to have been firm and close, with not much motion."

Williston figured (fig. 5*K*) the pes of UC 1708 with both tibia and fibula, the former of which seems to have disappeared sometime during the forty years of its residence in museums. Many of the elements are present only in outline, but the new and newly uncovered tarsal materials permit rather accurate comparison and identification. Williston correctly recognized the calcaneum. He drew an element which he labeled astragalus and shortly distal and postaxial to it another element — in outline on the matrix — which he did not label. We can now be certain that this outline represents the condyloid corner of the astragalus. Williston's "second, third, fourth and fifth" distal tarsalia are the first, second and third distal tarsalia and the preaxial part of the cuboid. The first metatarsal is lacking; what Williston drew as the fifth metatarsal is really the fourth.

Williston's figure (fig. 4*M*) of a free "calcaneum" is actually of the medial surface of an immature pubis showing the unbridged obturator foramen ("notch for the perforating artery") and the lateral pubic tubercle.

The phalangeal formula 2-3-4-5-4 in Williston's later (1925, fig. 155*A*) restoration of the hind limb is probably correct but is without foundation in material evidence.

MEASUREMENTS

The Chicago materials include a good number of immature bones — vertebrae, pelvic elements, pro- and epipodials. Williston (1914) figured an immature femur (fig. 5*D*), iliac blade (fig. 4*L*, as a "clavicle") and pubis (fig. 4*M*, as a calcaneum"). The present paper includes a figure of an immature vertebra.

It might be remarked, again, that the long bones seem either to have or not to have epiphyses, there being no intermediate stages observable. This is not necessarily evidence, however, for the presence of secondary centers of ossification; the materials may simply lack elements at the intermediate stages. This is quite possible when it is considered that there is a distinct gap in size between the largest of the (at least twelve) specimens of the best represented immature element, the femur, and the smallest femur equipped with epiphyses of which the ends have been well preserved. Measuring the proximal portions of the two femora — no immature femur has been preserved whole — the distance between the proximal end of the postaxial border and the tip of the internal trochanter is 7.2 mm. in the immature femur and 9.1 mm. in the ''subadult'' one; this implies a substantial difference between the lengths of the two.

The variation among the preserved elements in their degrees of attained growth created some difficulty during the reconstruction of a single, complete skeleton. This variation exists within the collections of all three museums, but there are some differences, the Chicago materials including many more of the obviously immature elements and the Harvard materials including some larger than average elements. Some idea of the range of variation may be gained by measuring the distance between the proximal end of the postaxial border and the tip of the pectoral crest in a series of humeri. For sixteen humeri, this measurement is (in mm.): 5.6 (UC), 7.4 (UC), 7.8 (UC), 8.6 (UC), 9.2 (UC), 9.3 (UC), 11.3 (AMNH), 11.5 (MCZ), 11.7 (AMNH), 12.7 (MCZ), 13.2 (UC), 13.4 (UC), 13.5 (UC), 14.2 (UC), 15.4 (MCZ), 16.2 (MCZ). There is no reason to suppose that the greater average size of the Harvard elements indicates a transition from a larger Wichita species to a smaller Clear Fork species. The difference is undoubtedly due to sampling error, the lower average size of the Chicago materials being a result of the presence of obviously immature elements and the simple lack of preservation of the larger individuals of *Araeoscelis gracilis*. This becomes quite clear when we consider that the two humeri in the American Museum Collection, found in the formation below the Harvard materials, are smaller than some in both the Harvard and Chicago collections.

In trying to arrive at a composite picture of an individual of

Araeoscelis whose size would come as closely as possible to that of what was likely the "average adult," I have chosen a size which lies between that of the "subadult" skeletons UC 659, 660, and 662 and that of the skeleton represented by the largest Harvard limb bones. Such an individual, I feel, would have propodials about equal in dimensions to the largest humerus and femur in the Chicago collection; these seem to be of a size about average, excluding the obviously immature elements, for the aggregate of the materials. With an eye to proportions in the "subadult" skeletons, I have tried to select the sizes of the other elements to reasonably fit a skeleton which would contain these propodials. In some cases, it was possible to find a preserved element judged to be of the proper size; in other cases, a slightly off-size element had to be drawn and the drawing then enlarged or reduced to the proper size. It can hardly be claimed that the results of this system must be absolutely accurate, but I believe that the proportions used in this paper — as recorded in the figures of the individual elements and of the complete skeleton and as tabulated below — come very close to the actual situation. In the following table, I have, for each entry, used the number of significant figures which the particular case warrants. I have presented those measurements which, I feel, are most likely to be of use to the reader in forming an idea as to the average size and proportions of an adult specimen of *Araeoscelis*.

Skull (exclusive of the mandible)[1]	
Length	42
Height	
At the naris	4
At the orbit	13
At the jaw articulation	17
Width (across skull's ventral surface)	
At the naris	7
At the orbit	20
At the jaw articulation	24
Mandible	
Length	42
Height	
At the jaw articulation	4.5
At the coronoid process	9.5

[1] All measurements are in millimeters.

Vertebrae

Length of the cervical series	?103.8
Lengths of the individual cervicals (number and positions uncertain)	

C1	4.3	C6	13.0
C2	10.6	C7	12.0
C3	12.5	C8	10.0
C4	15.7	C9	9.5
C5	15.7		

Length of the dorsal series	176.0
Length of the average dorsal vertebra	8.0

Pectoral girdle

Greatest overall height	36
Height through the glenoid fossa	16
Height of scapula	19
Length of coracoid plate	39
Distance between glenoid fossae	29

Anterior limb

Length of:

Humerus	57
Radius	?52
Ulnare	6.3
Fourth distal carpal	3.1
Third metacarpal	12
Fourth metacarpal	?15

Pelvic girdle

Greatest overall height	21
Length of iliac blade	19
Length of puboischiadic plate	42
Distance between acetabula	25

Posterior limb

Length of:

Femur	64
Tibia	62
Calcaneum	7.5
Cuboid	4.0
Fourth metatarsal	25

General body measurements

Length of neck, anterior to clavicles	?91
Glenoacetabular length	163

PHYLOGENETIC RELATIONSHIPS OF ARAEOSCELIS

THE EVIDENCE OF THE EAR

The Basic Dichotomy of the Reptiles

Goodrich, in 1916, developed the concept of a basic dichotomy in the ancestral reptilian stock. (The same concept had been implied in an earlier (1914a) paper of Watson.) He recognized a basal group, the Protosauria — retaining an anapsid temporal region — and two derived groups. One, the Sauropsida,[1] might be called the "true" reptiles; this group led to the Aves. The other group Goodrich termed the Theropsida; this group led to the Mammalia. As Goodrich (1942, p. 308) pointed out, "The general conclusion that the Reptilia have diverged into these two main branches with synapsidan and diapsidan skulls had already been accepted by many authorities. . . ."

Goodrich's evidence based on the structure of the heart (best summary: 1930) is now classic. The sauropsid circulatory system must have diverged early from that of theropsids. The presence of a single, right systemic arch in birds is but the completion of a basic sauropsid character. Considering the modes of separation, in the amniotes, of the venous and arterial streams, it seems most improbable that the theropsid system, with a single, left systemic artery, was derived from the sauropsid condition — where there are two systemic arteries, the right already singled out as the main carrier of aërated blood. Goodrich (1930, p. 577): ". . . the . . . completion of the interventricular septum and separation of the venous and arterial streams was carried out independently along two diverging phyletic lines. . . ."

Goodrich also believed in a second major evidence for dichotomy — the build of the fifth metatarsal. The fifth metatarsal of sauropsids, exceptions to be noted later, has a singular, hooked shape; it has a strong preaxial process which articulates with the fourth distal tarsal (the fifth distal tarsal tends to be reduced in sauropsids) at a level proximal to that of the other metatarsals. Goodrich (1916, p. 264): ". . . the hook-shaped metatarsal does not seem to be closely related to any particular mode of life or method of progression. . . ." Goodrich believed, there-

[1] To avoid confusion with the term Sauropsida as Huxley used it — to include all reptiles and birds — it might be best to use, as Goodrich (1930) has done, the compound term Reptilia Sauropsida.

fore, that it might serve as an important key character. He also suggested that the hook-shaped metatarsal might be related to the development of the mesotarsal articulation characteristic of birds and Reptilia Sauropsida.

Schaeffer (1941) discussed the evolution of the mesotarsal joint. He found it to be the functional joint in Chelonia and in the orders descended from the Eosuchia; he did not find it in the eosuchians themselves. Schaeffer found retention of a primitive pattern in mesosaurs, ichthyosaurs, sauropterygians and protorosaurs; the first three of these may be put aside due to their obvious aquatic modifications. Pelycosaurs, therapsids and mammals have a crurotarsal ankle articulation. The lack of a mesotarsal joint in eosuchians may be associated with the fact that the Eosuchia is a transitional group — it was in *Youngina* that Goodrich (1942) met with difficulty in his fifth metatarsal criterion. The lack of a mesotarsal joint in protorosaurs is disturbing, inasmuch as *Protorosaurus* has a hooked fifth metatarsal; however, Schaeffer felt their mode of ankle flexure to be primitive. It is interesting here that Camp (1945) thought *Protorosaurus* to be an eosuchian. As we shall see, the mesotarsal articulation is not a universally applicable key, but it may be used, in a general way, for the later sauropsids as compared with later theropsids.

Amidst confusion on the basic phylogeny of the Reptilia, Watson seized upon the structure of the middle ear as a major key to interpretation of relationships. Watson was not the first to consider this key; he is, however, responsible for its current emphasis and for the framework of a plausible history of the evolution of the middle ear. As I shall show, I do not agree with all of Watson's ideas, but I do accept his major evidence — the nature of the otic notch. I feel that the differences between the middle ears of modern reptiles and mammals can be seen as satisfactorily explicable by an eclectic theory — to be developed below — which utilizes certain other ideas, especially some of Westoll's, in combination with the basic theories of Watson.

The Middle Ear of Reptiles and Mammals

Many workers were involved in setting up the accepted homologies of the ear ossicles, but the whole thesis has become known as the Reichert-Gaupp theory. The definitive study is that of Gaupp (1913); Goodrich (1930) has given an excellent summary.

It would be hard to improve on the following description, from Goodrich (1930, p. 451), of the situation in a living reptile: "The typical columella auris extends from the fenestra ovalis of the auditory capsule to the tympanic membrane. . . . It consists, in the Lacertilia, of a proximal or stapedial region (stapes), and a distal extra-stapedial region (extra-stapes), generally called the extra-columella. The stapedial region is made up of a bony rod with a cartilaginous foot-plate embedded in the membrane closing the fenestra ovalis. The cartilaginous extra-stapedial region has its expanded outermost part embedded in the tympanic membrane; it also bears a processus internus (quadrate process) passing downwards and forwards in the roof of the tympanic cavity, and a more important processus dorsalis (supra-stapedial of Parker, and pr. paroticus of Gaupp). This latter dwindles to a ligament in the adult, except for its upper end, which remains as a nodule (intercalary of Versluys) lodged between the quadrate and paroccipital process (crista parotica) of the auditory capsule. A strong ligament passes from the dorsal process to the outer side of the extra-stapedial." There are some variations, e.g., the quadrate process may be lost, the base of the stapes may be pierced by the stapedial artery.

The columella is developed from the dorsal portion of the hyoid arch; it is homologous with the hyomandibular of fishes. In the embryonic lizard ". . . cartilage . . . appears in the proximal region of the stapes, in the dorsal process, in the extra-stapedial, and in the more ventral cornu of the hyoid arch. The proximal cartilage spreads outwards, forms the internal process, and becomes connected with the dorsal process; this whole region is known as the otostapes. . . . The outer extra-stapedial element forms the processus inferior inserted in the typanum, a small interhyal process, and grows inwards to meet the otostapes, from which it is distinguished as the hyostapes. The procartilaginous connexion of the hyoid cornu with the interhyal process dwindles to a mere ligament. In later stages the hyostapes fuses with the otostapes, the proximal region of the latter ossifies as a slender rod (stapes). . . ."

Turning to mammals, we find that the columella auris of reptiles has been functionally replaced by a chain of three ossicles connecting the fenestra ovalis with the tympanic membrane. There have been conflicting opinions (e.g., Gadow 1901,

Allis 1919) but most workers feel the following homologies to be well established: The mammalian stapes represents the reptilian otostapes, the incus of mammals is the quadrate of reptiles, and the mammalian malleus (pars) is derived from the reptilian articular. Mammalian embryos (cf. figs. in Goodrich and in de Beer 1937) demonstrate, with great clarity, the primitive, reptilian arrangement of these bones. The dermal part of the processus Folii of the malleus is formed by a bone homologous, according to Gaupp (1913), with the reptilian prearticular; there is, however, some disagreement on this homology (e.g., Olson 1944, Westoll 1944, 1945).

The tympanic bone, encircling the tympanic membrane of mammals, is homologous with the reptilian angular (Palmer 1913).

The M. tensor tympani is derived from the reptilian M. pterygoideus; the M. stapedius is derived from a slip of the M. depressor mandibulae (summary in Goodrich 1930).

Certain details of mammalian embryology will be pertinent in later discussion but are best deferred until after presentation of Watson's ideas.

Watson's Theory on the Evolution of the Ear

Watson's ideas on the evolution of the otic notch have been published at several times (earliest: 1914a). His book of 1951 is his most comprehensive recent statement on the subject.

Watson's basic ideas: In the earliest reptiles, for some reason or other — probably a matter of a more effective jaw brace — a vertical quadrate bone was more advantageous to the animal than one that was not vertical. Beginning with a labyrinthodont amphibian, the two lines of Reptilia can be seen to be derived as follows (Watson 1951, p. 116): 1) ". . . the upper end of the quadrate remains fixed and the lower end is swung forward. By this process the otic notch is preserved and indeed widened out . . . and the end of the stapes, with all its processes, remains as it was. This condition is found in *Diadectes* . . . and is preserved in many later reptilian orders, including all those which have still-living members. This group ends in the birds." This group is the Reptilia Sauropsida of Goodrich. 2) "The other way in which the quadrate can become vertical is by keeping the lower end fixed and moving the upper end backward. . . .

The otic notch is entirely obliterated and the tympanic membrane, if it were to survive at all, would have to change its position. These modifications eventually change the whole arrangement at the outer end of the stapes. The disappearance of the tympanic membrane abolishes the possibility of a transmission of its vibrations through the stapes to the ear. . . .'' In these reptiles, the stapes gained a new contact with the quadrate, and hearing took place, as in snakes, by transmission of sound vibrations through the bones of the skull. This second group of reptiles is the Reptilia Theropsida of Goodrich.

Romer (1946, p. 176), however, discussing the otic notch of *Diadectes,* found it ''. . . difficult to understand, on the assumption that the diadectid notch is essentially primitive, why the quadrate and paroccipital go out of their way (so to speak) to articulate at a point far from the direct line between occiput and quadrate.'' On the grounds of this difficulty, Romer felt that the diadectid otic notch might be a new development retaining the quadrate-braincase connection acquired at the *Limnoscelis* stage. Romer retracted this theory in 1950, and Watson (1951) presented some counterarguments: 1) The laterally placed fenestra ovalis of *Diadectes* (Olson 1947) recalls that of *Seymouria* and could not well be derived from a captorhinomorph stage; this feature may, however, be of independent development. 2) The Diadectomorpha, including, along with *Diadectes* and pareiasaurs, the procolophonids — among them *Nycteroleter* and *Nyctiphruretus* (Efremov 1940) — seem to be a group of genuinely related animals. It seems impossible to redevelop, secondarily, the labyrinthodont-like occiput of *Nyctiphruretus* from such a form as *Limnoscelis;* it could, however, be quite easily derived from a *Seymouria*-like form.

Starting with the diadectid-like otic notch of the early sauropsid reptiles, Watson felt it a simple matter to derive the condition seen in later sauropsids. The columella auris of the sauropsids is completely homologous with that of labyrinthodonts; this has been demonstrated for several labyrinthodonts (figs. in. e.g., Parrington 1948, Watson 1953). The sauropsid tympanic membrane is simply an expanded labyrinthodont tympanic membrane.

It is in the derivation of the mammalian middle ear from that of early theropsids that complexities appear.

Watson delivered the Silliman Memorial Lectures at Yale in 1937. These lectures were published, with extensive addenda, in 1951. Some statements in the addenda contradict statements in the original lectures. It is important, for the present purpose, that we review both the original and the modified opinions of Watson.

Watson, in his original lectures, noted the presence of a slender extension — similar to a hyostapes — of the stapes of gorgonopsids. This extension projected laterally beyond the stapedial-quadrate contact to insert, Watson believed, into a small tympanic membrane which may have laterally closed a cylindrical hollow crossing the posterior surface of the quadrate. Watson thought that this membrane might have become coextensive, in cynodonts, with a new membranous growth stretched across the two limbs of the angular and lying lateral to the articular. Sound vibrations would have been conducted to the membrane by an external auditory meatus which lay in a groove along the posterior border of the squamosal.

Watson later (1951, appendix to chap. 6) stated that further preparation had disclosed that the gorgonopsid stapes ended at the quadrate and had no hyostapes-like extension. Watson added that gorgonopsids probably had no remnant of the original, labyrinthodont tympanic membrane, that the groove in the gorgonopsid squamosal need not be homologous with the external auditory meatus of cynodonts, that the tympanic membrane of mammals is probably a completely new, secondary development, and that it is useless to look for a hyostapes in the mammalian embryo.

Watson (1948) had already expressed his opinion that there was no tympanic membrane in pelycosaurs.

In his latest (1953) word on the evolution of the mammalian ear, Watson reiterates his conviction that there was no tympanic membrane in pelycosaurs; he also believes there was probably none in captorhinomorphs. He bases his opinions on several facts: 1) In these forms, there was an extensive stapedial-quadrate contact. This is an established fact for *Captorhinus* (e.g., Sushkin 1927), and the stapedial recess in pelycosaurs very probably housed a cartilaginous extension of the stapes. 2) The stapes was probably too large to be actuated by a tympanic membrane. Romer and Price (1940) recognized this difficulty in pelycosaurs. This is not too effective an argument and applies

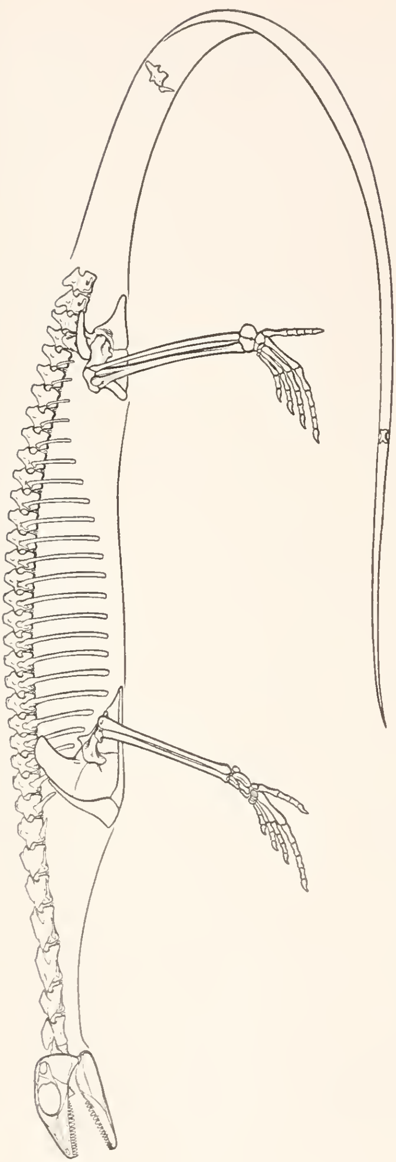

Fig. 15. Skeletal reconstruction of *Araeoscelis*; composite; atlantal neural arch, most of the ribs, and phalanges restored. x 1/3.

only to those pelycosaurs with massive stapes; Watson does not rely too heavily upon it. 3) There was no place on the skulls of theropsids where a tympanic membrane might have been placed. Watson (e.g., 1948) considers this a very strong argument, and, indeed, if one thinks in terms of a laterally placed, sauropsid-like tympanic membrane, it does seem impossible that the theropsids might have had one. I shall return to this point.

Watson (1953) was definite in his statement that the stapes of pelycosaurs, and of *Captorhinus,* is completely homologous with that of labyrinthodonts and sauropsids; he felt that a ligament along the ventral edge of the pelycosaurian stapes, passing ventrally to be attached to the pterygoid process of the quadrate, is homologous with the hyoid process of the sauropsid stapes. The essence of this contention of Watson's is that there was no hyostapedial projection lateral to the stapedial-quadrate contact.

Watson considered the new, "mammalian" tympanic membrane to have been already developed in cynodonts, and there stretching across the inner end of an external auditory meatus which lay in a groove on the posterior portion of the squamosal. He stated (p. 173) : "This membrane . . . may well have lain in a plane which would touch the outer surface of a large process, which exists in some specimens of *Gomphognathus* for attachment of the posterior pterygoid muscle to the articular, and continue to include the outer surface of the reflected lamina [of the angular]. Such a plane might well have been on a thin sheet of tissue, not necessarily of the structure of a tympanic membrane, which separated an air-filled extension of the tympanic cavity from the outer air." Watson felt that this thin sheet of tissue probably played little part, in *Gomphognathus,* in the transmission of sound waves but that the anterior extension of the tympanic cavity probably acted as a resonating chamber. When the quadrate and articular, with evolution, were freed of heavy muscle stresses, the bone conduction of sound in theriodonts gave way to the so-called air conduction system of mammals and vibrations of the tympanic membrane were transmitted to the fenestra ovalis. Watson assumed that the original tympanic cavity — of labyrinthodonts — survived through the theropsids even though the original tympanic membrane was lost.

Critique of Watson's Theory and Remarks on Westoll's Contributions

Watson's explanation of the method by which the shifting of the jaw muscles, due to a general reduction in skull height, relieved the hinder part of the jaw of large bending stresses is a valuable contribution to our knowledge of how the quadrate came to be able to take part in the mammalian system of sound transmission. The tympanic membrane is, undoubtedly, a new, secondary development — in great part.

The disturbing feature of Watson's paper is his contention that an outgrowth of the stapes seen in theriodonts (figs. in Broom 1936, Olson 1944, Parrington 1946a), similar to a hyostapes, is a *new* development, connecting the stapes with the new membrane. It is difficult to see any advantage in this ''new'' development. It is obviously the same sort of outgrowth that Watson described in his original Silliman lectures. We may ask whether this stapedial outgrowth may not well be the labyrinthodont hyostapes, as Broom, Olson and Parrington have held it to be, and, if it is, whether the theriodonts might not also have retained a remnant of the labyrinthodont tympanic membrane.

Certain details of mammalian embryology are pertinent to this objection to Watson's thesis. There *are* signs of a hyostapes in mammalian embryos. Van der Klaauw (1923) discussed the cartilages of Paauw and Spence. According to van der Klaauw, Paauw's cartilage, in the tendon of the M. stapedius, is a part of the hyostapes, and Spence's cartilage is a homologue of the processus internus of the reptilian stapes. Westoll (1944) regards Spence's cartilage as the remains of the tympanic portion of the hyostapes, and, indeed, the position of its ossification, as we shall see later, bears Westoll out.

Goodrich (1930, p. 458) summarizes the developmental connections of the mammalian stapes: ''The top end . . . is bent at an angle so that its innermost extremity is continuous with the tissue closing the fenestra ovalis. . . . Here develops the stapes, as a ring round the stapedial artery, and it chondrifies separately from the ear capsule [except, perhaps, for a peripheral ring which completes the stapedial plate; c.f., e.g., Reagan 1915]. The more distal (interhyal of some authors) 'hyostapedial ligament' remains for a time uniting the stapes to the dorsal

end of the 'laterohyal' ('tympanohyal') region of the hyoid cornu, but disappears later. Meanwhile, the laterohyal and more ventral region of the cornu form a continuous cartilage which fuses with the paroccipital process of the auditory capsule. Later the dorsal region of the cornu below the laterohyal degenerates into a ligament, leaving, however, in man a considerable portion to form the styloid process. . . ." The laterohyal region in mammals is homologous, at least in part, with the processus dorsalis of the reptilian columella (cf. discussion and figs. in de Beer 1937).

Very important is the course of the N. chorda tympani. Goodrich (1915) studied the embryonic relationships of this nerve. In both embryonic and adult reptiles, the facial nerve, after passing through the facial foramen, gives off a palatine branch, runs above the columella, passes posterior (and medial) to the dorsal process of the stapes, and gives off the chorda tympani. The chorda tympani passes forward, dorsal to the hyostapes and tympanic cavity, to run down the posterior surface of the quadrate to the medial side of the articular.

In the adult mammal, the chorda tympani runs forward in the posterior malleolar fold and then passes between the manubrium of the malleus and the long crus of the incus before making its lateral exit; this part of its course will receive further attention below. The facial nerve typically passes medial and posterior to the laterohyal. There are some exceptions to this typical placement of the nerve with respect to the laterohyal; van Kampen (1905) and Gaupp (1913) offer explanations.

Goodrich (1915) stressed that the chorda tympani of amniotes is posttrematic but pretympanic. The spiracular slit does not contribute to the tympanic diverticulum; the diverticulum is a ventral outgrowth of the hyomandibular pouch.

The studies of Romer (1937, 1941), Eaton (1939), and Westoll (1943) have helped to establish the hyomandibular bone of crossopterygian fish as completely homologous with the columella auris of reptiles. The hyomandibular has two processes for braincase articulation; Romer, Eaton and Westoll have demonstrated that the more ventral of these two processes is the homologue of that part of the otostapes which is fitted into the fenestra ovalis. The more dorsal of the two processes is the homologue of the processus dorsalis of the reptilian columella. The hyo-

mandibular has an opercular process; this gave rise to the tympanic portion of the hyostapes. The ventral end of the hyomandibular bore two cartilaginous (or ligamentous) extensions: one, connected to the quadrate, became the quadrate process (internal process) of the reptilian columella; the other, connected to the hyoid, gave rise to the hyoid process (interhyal process) of the reptilian adult and the mammalian embryo.

Romer (1941) showed that, in *Ectosteorhachis* (''*Megalichthys*''), the facial nerve entered the proximal portion of the hyomandibular and divided into a mandibular ramus (chorda tympani) and a hyoid ramus. These rami emerged about halfway down the length of the hyomandibular and continued ventrally along its lateral surface.

Westoll (1943) supported and elaborated the concept of the transformation of the rhipidistian hyomandibular into the reptilian columella. He held that the original, labyrinthodont tympanic diverticulum was directed dorsally and lay anterior to the chorda tympani (The chorda tympani is posttympanic in Anura.); this fits in nicely with Romer's description of the nerve channels of the hyomandibular. With closure of the otic notch, according to Westoll, this dorsal diverticulum was forced ventrally, the chorda tympani came to lie dorsal to the tympanic cavity, and a new extension of the hyomandibular pouch (p. 408) ''. . . thrust between the quadrate and ceratohyal connexions of the stapes, reached up toward the extrastapes (processsus tympanicus) and also spread round the processus quadratus to meet the dorsal diverticulum. . . .'' In this way, Westoll felt, the tympanic cavity of early reptiles became expanded, the labyrinthodont tympanic membrane was retained, and the hyostapes — forced ventrally by the downturning of the tabular and the paroccipital process — persisted in its insertion into this membrane; such a history would account for the typical condition seen in the middle ears of living reptiles. The condition in mammal-like reptiles is then derived by modification of this basic patern. Thus, under Westoll's scheme, there would be no need to consider reptilian phylogeny as basically dichotomous.

In the evolution of mammal-like reptiles, according to Westoll, the tympanic diverticulum moved further ventrally, and a new, ventral extension (''recessus mandibularis'') of the tympanic

cavity was formed, at first (p. 393) "... applied to the lower inner surface of the mandible and later accommodated in a special cavity bounded by the reflected lamina of the angular." The major portion of the mammalian membrane would be a new development, but the postero-dorsal portion would be homologous with the labyrinthodont tympanic membrane. The quadrate contact of the stapes would be emphasized, but the hyostapes would be retained in theriodonts and in mammalian embryos.

In 1945, Westoll elaborated on the composition of the mammalian membrane: Schrapnell's membrane (the "pars flaccida" of the tympanic membrane) represents the remains of the labyrinthodont membrane; it is the membrane to which the hyostapes of therapsids was attached. The Chordafalten (malleolar folds) of Bondy represent compressed tissues which separated the dorsal (labyrinthodont) tympanic diverticulum of therapsids from the mandibular recess of the tympanic cavity. Spence's cartilage, which gives rise to Bondy's Chordafortsatz,[1] is a separated, distal part of the hyostapes; its relation to Schrapnell's membrane indicates that it was probably the tympanic portion of the hyostapes.

Gaupp (1898, e.g.) had already expressed doubt as to complete homology of the sauropsid and mammalian tympanic membranes. Gregory (1910), discussing the significant fact that the membrana propria of the mammalian pars tensa is absent from both the mammalian pars flaccida and the reptilian tympanic membrane (Versluys 1899, Denker 1901), had suggested that Schrapnell's membrane might be homologous with the sauropsid membrane. Gregory (1929, e.g.) had also suggested the presence of a tympanic diverticulum associated with the angular.

Toward a Reconciliation of the Theories of Watson and Westoll

Westoll's ideas do not satisfactorily account for certain pertinent details in the course of the chorda tympani. Westoll assumed that, in the common reptilian ancestor of both living reptiles and mammal-like reptiles, the chorda tympani lay dorsal to the original, labyrinthodont tympanic diverticulum and that

[1] Bondy's Chordafortsatz, present in ossified or cartilaginous form, conducts the chorda tympani through the posterior Chordafalte to the malleus (van der Klaauw 1931).

this diverticulum terminated laterally at a tympanic membrane. It is not clear, under his scheme, just how the chorda tympani came to this dorsal position from the ventral (posterior) position which it had occupied in labyrinthodonts. Further, after having attained this dorsal position, the chorda tympani would have had to move ventrally again, through — or across — the pars flaccida to reach the position which it occupies in mammals — between the pars flaccida and the pars tensa.

Study of the many figures of this region, in adult and embryonic mammals, published by Bondy (1907, 1908) will show that the chorda tympani runs, invariably in at least the embryo, along the Chordafortsatz (if present; cf. van der Klaauw 1931) through the posterior Chordafalte. The chorda tympani seems, generally, to lie somewhat ventral to the Chordafortsatz (van der Klaauw 1923); if Spence's cartilage represents the tympanic portion of the hyostapes, this would suggest that the chorda tympani lay ventral to the hyostapes in the theropsid ancestor of mammals. In the adult mammal, it is impossible to say which is morphologically the more dorsal, stapes or chorda tympani; the distal end of the stapes does not reach the vertical plane of the nerve. In actual elevation, the chorda tympani of, e.g., man is situated dorsal to the stapes while the Chordafortsatz of the domestic cat may easily be seen (when preserved) to lie ventral to the stapes. Truscott and Struthers (1941) described the chorda tympani of the embryonic *Microtus* as arising from the facial nerve immediately anterior to the first branchial groove and then passing *behind* the stapes to extend along the path of the developing mandibular arch. The description of the chorda tympani of mammals (Goodrich 1930, e.g.) as morphologically dorsal to the stapes is arbitrary and based on preconceived notions of homology of sauropsid and mammalian tympanic diverticulae. That the nerve may lie dorsal to the hyostapedial connection between stapes and hyoid cornu in embryonic mammals (cf. de Beer 1937, pl. 141, figs. 21-24) is no argument for a position of the chorda tympani dorsal to an ancestral hyostapedial-Schrapnell's membrane contact; in sauropsids (cf. *op. cit.;* pl. 140, fig. 12; pl. 141, figs. 13, 14, 16, 17) the tympanic process of the hyostapes projects laterally from the parasagittal plane of hyostapedial-hyoid cornu contact. Again, as already noted, the chorda tympani tends to lie ventral to Spence's carti-

lage — the probable tympanic portion of the hyostapes.

The Chordafalten — and Chordafortsatz — separate the epitympanic recess (attic) from the tympanic cavity proper of mammals; this is the case in at least the embryo. Schrapnell's membrane forms the non-osseous portion of the lateral wall of the attic. These relations hold regardless of proportions: in swine, deer, etc., both the attic and the pars flaccida are very large, the pars flaccida larger than the pars tensa in swine (Bondy 1907); in lower primates, the attic attains considerable size (Lambert 1949). If Schrapnell's membrane is homologous with the sauropsid (and, therefore, labyrinthodont) tympanic membrane, how does it happen that in mammals the chorda tympani lies ventral to this membrane while in the sauropsids the chorda tympani runs dorsal to it? The answer will, I believe, help demonstrate the validity of the Goodrich-Watson argument for early reptilian dichotomy.

The crossopterygian chorda tympani (ramus mandibularis internus facialis) was, as it is in tetrapods, posttrematic. It is not known at what evolutionary stage between crossopterygian and reptile the tympanic diverticulum first appeared. Further, the function of this original diverticulum is obscure; it might have freed the hyomandibular somewhat for a crude type of hearing. At any rate, this diverticulum (the dorsal diverticulum of Westoll 1943) came to lie anterior to the chorda tympani and to incompletely surround the hyomandibular — which lay above and behind the developing cavity. At an early stage of development of the tympanic cavity, the "tympanic membrane" must still have been quite thick; it is improbable that the diverticulum, immediately upon its inception, made contact with the skin.

Let us consider, first, the evolution of mammals from this early condition. The tympanic cavity, upon expansion, reached the skin, and a two-layered tympanic membrane was formed. I agree with Westoll that the situation in Anura may easily be seen as derived from such a stage, but after this point, I disagree with him in certain important particulars. With otic notch closure and downturning of the paroccipital process and tabular, the tympanic diverticulum, tympanic membrane (Schrapnell's membrane) and the hyostapes were undoubtedly driven ventrally, but they drove the chorda tympani before them. In the later stages of evolution to the mammalian condi-

tion, a new, more ventral diverticulum (recessus mandibularis of Westoll 1943) pushed out ventral to the chorda tympani to the region of the angular, and the lateral wall of this extension of the tympanic cavity gave rise to the stratum mucosum of the pars tensa. The chorda tympani became trapped between dorsal and ventral diverticulae; the very position of the ventral diverticulum — directed toward the angular — explains its relation to the nerve. The picture in the late therapsids must have been this: The otostapes was in contact with the quadrate which articulated with the articular which had become fastened in the developing pars tensa. The hyostapes projected posterolaterally from the stapedial-quadrate contact to be inserted into Schrapnell's membrane. The chorda tympani passed forward between Schrapnell's membrane and the pars tensa, and, in so doing, passed between the hyostapes-pars flaccida contact and the articular-pars tensa contact.

This history accounts for the presence of the chorda tympani in the posterior malleolar fold and, as would Westoll's scheme also, its position ventral to the chain of auditory ossicles.

It is difficult to continue the comparison of the labyrinthodont dorsal diverticulum with the epitympanic recess of mammals. The embryology (cf. Bondy 1908, Bast and Anson 1949) is not too clear; as I understand it, it is mainly a matter of the clearing away of mesenchymal cells. According to Bast and Anson, the pneumatization of the attic lags behind that of the tympanic cavity proper; this, combined with the fact that the chorda tympani is in position near the Chordafortsatz before the tympanic cavity reaches the region of the auditory ossicles (cf., e.g., van der Klaauw 1923, figs. 2, 3), may account for the observation of Goodrich (1915) that the nerve is completely pretympanic in all amniotes. It may be that future work will distinguish between two diverticulae of the hyomandibular pouch, one dorsal to the chorda tympani and one ventral to it.

Westoll (1945) felt that Schrapnell's membrane in mammals bears the same relations to the bony walls of the attic that the "reptilian" tympanic membrane bore to the corresponding part of the therapsid bony skull. As Westoll indicated, the main change required is that the Schrapnell's membrane of therapsids had, in evolution to mammals, to make contact with the anterior

limb of the tympanic bone; this was an easily accomplished shift in position.

To derive the sauropsid condition, we must return to that stage in which the tympanic cavity had not yet touched the skin and the "tympanic membrane" was still quite thick. We might consider two alternatives:

Alternative 1). The chorda tympani arose from the facial nerve at a point considerably dorsal to the corresponding place of bifurcation in "pre-theropsids." The dorsal tympanic diverticulum, on reaching the skin, came, directly, to lie ventral to the chorda tympani. This process is not too difficult to visualize when one considers that the hyomandibular pouch probably took origin from the pharynx at a place ventral to the origin of the chorda tympani and that, as in embryos of recent forms, the proximal portion of the hyomandibular pouch was not much expanded. This alternative suffers, however, from lack of any evidence that might show reason for such a process.

Alternative 2). The following theory was suggested by Goodrich (1930, p. 484) to explain the derivation of the condition in all amniotes from that of the amphibian. I shall use it to explain the derivation of the sauropsid condition: ". . . the presence of a tympanic notch and a columella in the Stegocephalia is clear evidence that these primitive tetrapods, not far removed from the common ancestor of both modern Amphibia and Amniota, already possessed an auditory apparatus provided with a tympanum . . . we [may] suppose that there has been in the ancestral Amniota a shifting downwards of the tympanum and forwards of the chorda tympani across the tympanum perhaps at a time when this membrane was still thick."

There is a reason why the chorda tympani probably moved as Goodrich suggested. Watson's suggestions in regard to the otic notch enter here: The forward movement of the ventral end of the quadrate, removing the hind end of the mandible to a more anterior position, would account for the forward movement of the chorda tympani through a thick tympanic membrane; subsequent thinning of the membrane probably forced the nerve farther anteriorly, to the posterior surface of the quadrate. It is significant here that, in fossil (Williston 1925) and in living (Willard 1915, Goodrich 1930) reptiles, the chorda tympani runs for a distance within the lower jaw after passing through a

foramen in the prearticular, in the articular, or between the prearticular and angular bones.

Whether or not, considering their differential placement with respect to the chorda tympani, Schrapnell's membrane and the sauropsid tympanic membrane are to be regarded as strictly homologous is a technical argument I do not care to enter.

The ideas of Watson and of Westoll, with judicious modification of each, are seen to be consonant.

In the Reptilia Sauropsida, with expansion of the otic notch, emphasis came to be laid on the tympanic process of the hyomandibular. In the Reptilia Theropsida, with otic notch closure, emphasis was placed on the quadrate process of the hyomandibular and the tympanic process gradually fell off in importance. Since *Seymouria,* with a good otic notch, is so near the amphibian-reptilian border-line, the basic split in the reptilian stock may be looked upon as true dichotomy and need not be considered as diphyly. Watson (1951), and also Olson (1947), allied *Seymouria* with *Diadectes;* at least otic notch expansion need not have occurred until after the beginnings of the Reptilia. There is no reason to believe that both theropsids and sauropsids might not have been derived from the same general group of labyrinthodonts.

Examination of the detailed relations of the chorda tympani and Schrapnell's membrane lends support to the Goodrich-Watson theory of reptilian dichotomy.

Other Theories and Criticisms

Discussion of certain recent, radical ideas on ear evolution will aid in the study of the situation in *Araeoscelis.*

Tumarkin (1948a, b, c, 1949) tried to explain the evolution of the auditory conducting mechanisms of tetrapods on "functional" grounds. He assigned the mechanisms in modern animals to six groups; the classification is neat and the nomenclature clear. Using "vestibulo-" for the fenestra ovalis end of the chain, the groups are: 1) "vestibulo-squamosal," found among urodeles, 2) "vestibulo-quadrate," found among snakes, lizards, many extinct reptiles, 3) "vestibulo-scapular," found among urodeles, anurans, 4) "vestibulo-hyoid," amphisbaenids, *Sphenodon,* 5) "vestibulo-tympanic," found among anurans, crocodilians, turtles, lizards, 6) "vestibulo-ossicular," in mammals.

Tumarkin's major conclusions seem to be: 1) The labyrinthodonts had no fenestra ovalis; the otic notch, therefore, could hardly have supported a tympanic membrane. 2) Cotylosaurs — Tumarkin was thinking of captorhinomorphs — and pelycosaurs had no tympanic drum and no tympanic cavity; there had been no migration of a drum from the otic notch. 3) Mammals inherited the ''vestibulo-quadrate'' system of therapsids and went on to ''vestibulo-ossicular.'' 4) The ''vestibulo-squamosal'' of urodeles, ''vestibulo-quadrate'' of snakes and some lizards, and ''vestibulo-hyoid'' system of *Sphenodon* are *not* degenerate conditions. 5) The anuran middle ear is a new development.

Tumarkin's conclusions may be considered *seriatim*:

1) Parrington (1949), answering Tumarkin, pointed out that: a) Romer and Witter (1942) had demonstrated an open fenestra ovalis in the primitive labyrinthodont *Edops*. Later forms also had perforate oval windows. b) Although Watson (1926) had found no oval window in the Carboniferous *Eogyrinus* and *Palaeogyrinus,* he had found a pit in its place, and the stapes of one form terminated flush with the skull surface. Watson had suggested that hearing in an aquatic medium might be possible through a tympanic drum even with an imperforate fenestra ovalis, c) The properly articulated stapes of labyrinthodonts is directed toward the otic notch. d) Some forms, as *Tertrema* and *Cyclotosaurus*, had otic notches completely encircled by bone — apparently as independent developments.

Parrington concluded that the otic notch held a functional tympanic membrane.

2) Parrington accepted Westoll's ideas on the evolution of Schrapnell's membrane and pointed out Tumarkin's fundamental weakness; the latter's difficulties arose because he could not see how the sauropsid and mammalian tympanic membranes could be homologous and because he could not see how the malleus and incus came to be interpolated between fenestra ovalis and tympanic membrane. The answer to both of Tumarkin's difficulties is obvious in Westoll's work — the sauropsid tympanic membrane is homologous with only the pars flaccida of the mammalian membrane.

Parrington dismissed, as unsupported, Tumarkin's assertion that premammals heard via their buccal cavity.

Parrington felt that the evidences (including a hyostapes) for a fundamentally "reptilian" organization of the theropsid middle ear, discernible even through changes in emphasis on the different contacts, argued that a ventralward migration of Schrapnell's membrane from the otic notch, did, in fact, take place.

3) No one would argue against Tumarkin's assertion that mammals inherited the "vestibulo-quadrate" system of therapsids; such a system was a necessary forerunner of the incudo-stapedial joint.

4) Smith (1938) studied the middle ear of certain lizards (agamids, iguanids, chamaeleons) which seem to demonstrate the following evolutionary sequence: a) The tympanic membrane becomes covered by skin. b) The tympanic membrane and extra-stapedial structures disappear. c) The distal end of the remaining portion of the columella becomes united with the quadrate. d) The middle ear cavity is obliterated and the auditory cup of the quadrate disappears. The product of such a process may, for want of better description, be called by the classic term "degenerate."

Tumarkin thought that the pro-Squamata had "vestibulo-quadrate" hearing, that this type of hearing persists as a primitive condition in some lizards (e.g., chamaeleons), and that the "vestibulo-tympanic" system of lizards is a secondary development. Tumarkin's difficulty in this case is obvious; he thought lizards to be derived from captorhinomorphs, where, indeed, there was a good stapedial-quadrate contact. This difficulty is removed by the Goodrich-Watson scheme of dichotomy. Further, reference to figures of *Prolacerta* (Camp 1945), a reptile probably very near the origin of lizards, will show that there was adequate space for a large tympanic membrane. Smith has shown that, with complete disappearance of the tympanic membrane in lizards, the quadrate loses all posterior concavity; the quadrate of *Prolacerta* is posteriorly concave.

There is no reason why we cannot agree with de Beer (1937, p. 241) that the connection, in the adult *Sphenodon*, of the ceratohyal with the columella auris ". . . is . . . the persistence of an embryonic feature which represents no phylogenetically primitive condition, but must be associated with the degeneration of the tympanic membrane and therefore constitutes a sec-

ondary condition, brought about by arrest of development."

5) As Westoll (1943) has shown, the anuran ear is readily seen as derived from the condition in labyrinthodonts.

Tumarkin neglected the embryological and paleontological evidence for a theropsid hyostapes, was incorrect in his assumption that a perforate fenestra ovalis was absent in all labyrinthodonts, disregarded the evidence of the articulated labyrinthodont stapes, and failed to note that many workers (e.g., Gregory, Parrington, Watson, Westoll) do not regard the sauropsid and mammalian tympanic membranes as completely homologous.

Tumarkin objected to ideas of "degeneracy" used as an explanation for the conditions in many modern forms. However, we cannot, without sufficient evidence, allow ourselves the convenience of independent derivation of auditory structures to suit the particular needs of every group of tetrapods; Occam's razor makes ideas of "degeneracy" unavoidable.

I entertained, for a time, the notion that the stapedial-quadrate contact of the theropsids might have arisen in the following manner: Upon otic notch closure, the stapes came immediately to abut on the quadrate. Such a stage, I thought, might be illustrated in *Lanthanosuchus* (Efremov 1946) where a pit near the dorsal end of the quadrate might well have received the distal end of the stapes. With the downturning of the paroccipital process, I supposed the stapes to have been driven ventrally along the quadrate until it reached the position it occupies in captorhinomorphs and pelycosaurs. I saw the condition in *Nyctiphruretus* (Efremov 1940), where the stapedial-quadrate contact is rather high and where the paroccipital process is still directed dorsally, as the retention of an intermediate state.

It is, however, fairly well established (Efremov 1940, Watson 1951) that *Nyctiphruretus* is a procolophonid, and Romer (personal communication 1953) feels that *Lanthanosuchus* is a flattened procolophonoid. That Efremov grouped *Seymouria* and *Kotlassia* with *Lanthanosuchus* is no deterrent to this classification; since Olson (1947) and Watson (1951) both felt that *Seymouria* and *Diadectes* are closely related, *Lanthanosuchus* is either related to or a member of the Diadectomorpha. This diadectomorph relationship, plus the fact that the skulls of both *Lanthanosuchus* and *Nyctiphruretus* are highly specialized in many respects, make it exceedingly probable that the firm

stapedial-quadrate contact in these two genera is the result of a process of "degeneracy" somewhat similar to that which has given rise to the condition in chamaeleons.

The Tympanic Membrane and External Auditory Meatus in Theropsids

Parrington (1946a) showed that any tympanic membrane present in captorhinomorph reptiles must have lain behind the quadrate. In theriodonts (Parrington 1949), the bending outward of the zygomatic arch resulted in the formation of an external auditory meatus connecting the tympanic membrane with the exterior. Parrington presented evidence for a tympanic membrane posterior to the quadrate in cynodonts and (1946b) in gorgonopsids (cf. Broom 1936 for similar evidence in therocephalians); he interpreted the groove along the posterior border of the squamosal in both these groups as the path of the external auditory meatus. Parrington's analysis of the gorgonopsid picture agrees closely with the views of Watson as expressed in his original Silliman lectures.

Watson (1948) dismissed the possibility of a superficial, sauropsid-type tympanic membrane in pelycosaurs. Parrington (1949), however, brought in an alternative suggestion of Romer and Price (1940, p. 62) to possibly describe the case: ". . . the tympanum might reasonably have been situated somewhat below the surface in a vertical plane at right angles to the general direction of the stapes and thus diagonal to the long axis of the skull . . . the anterior margin of the drum would have been attached to the quadrate along a line passing downward internal to the quadrate foramen and thence to the inner, back corner of the articular region." Parrington thought that, if *Dimetrodon* had a tympanic membrane, the recession of the median component of the quadrate necessitated an external auditory meatus. This meatus may have made its way from above the inner of the two quadrate condyles to a more lateral and dorsal position, passing out beneath (anterior to) the upper part of the M. depressor mandibulae.

Schrapnell's membrane is but a vestige of a larger, labyrinthodont tympanic membrane; it is of no great aid to hearing in mammals and probably played but a very small part in the

hearing of early theropsids. Bone, as advocated by Watson (1951, 1953), probably provided the main route of sound conduction, and the evolutionary history of the theropsids must have seen a steady decrease in function of Schrapnell's membrane.

How efficient the theropsids' bone-conduction of sound may have been remains a problem. Snakes, with a bone-conduction system, are deaf to air-borne sounds but receive sounds conveyed through the ground to the body (Beatty 1932). Whales (discussion in Howell 1930) cannot receive sound through their lax tympanic membranes, but observation, the high development of their internal ears, and the size and character of their acoustic colliculi all indicate that they must receive sound waves through some solid part of the head. It is possible that the aquatic medium facilitates the cetacean mode of sound reception. Ophiacodonts were probably aquatic or, at least, amphibious (Romer and Price 1940) ; perhaps it was this early aquatic environment which permitted the pelycosaurian emphasis on bone-conduction of sound. It is most interesting in this connection that Romer (1948) has taken the view that ichthyosaurs, which had a middle ear fit only for bone-conduction, might have been derived from anapsid pre-ophiacodonts.

As Schrapnell's membrane, upon otic notch closure, moved ventralward to a deep position posterior to the quadrate, an external auditory meatus must have been formed. As Parrington suggested, the external end of the meatus was probably forced to remain in a dorsal position due to the presence of the M. depressor mandibulae. Watson (1948) has restored this muscle in *Dimetrodon*. His reconstruction shows it as a thin muscle with its origin on a posterior projection formed by the ventral ends of the tabular and supratemporal. Between the muscle and the posterior border of the squamosal lies a vertically elongate slit, wider above than below; the dorsal widening is enhanced by a gentle dip in the posterior border of the squamosal. The upper portion of the slit probably housed the external end of the auditory meatus. The course of the meatus may represent the path taken by Schrapnell's membrane during its ventralward displacement.

With early theropsid emphasis on bone-conduction of sound, the external auditory meatus most likely underwent a decrease

in the diameter of its lumen. However, with the appearance, in therapsids, of a mandibular resounding chamber and, later, of a new tympanic membrane and a vibratory chain of auditory ossicles, the external auditory meatus, still patent, was seized upon and enlarged, to leave its imprint, faintly in gorgonopsids and more strongly in cynodonts, on the posterior portion of the squamosal. The position of the external auditory meatus as it must have occurred in pelycosaurs is easily comparable to the position of the meatus in therapsids. Since the pars flaccida and pars tensa of the tympanic membrane must have come to lie in a common plane during the later phases of therapsid evolution, it is not hard to see how an external auditory meatus leading to Schrapnell's membrane came to conduct sound toward both the pars flaccida and the pars tensa.

The Middle Ear of Araeoscelis

The lateral view of the skull of *Araeoscelis* makes it immediately obvious that no sauropsid otic notch was present. Further, there is no space for a superficial tympanic membrane of the sauropsid type. The quadrate is hidden laterally by the squamosal, is posteriorly convex for most of its height, and has no auditory cup. The M. depressor mandibulae must have crowded very near the posterior border of the cheek, and the retroarticular process is almost nonexistent.

In occipital view, the position of the paroccipital process and of the fenestra ovalis, the form of the stapes with its processes, and the presence of a stapedial recess in the quadrate show clearly that the stapes was directed laterally, posteriorly and ventrally from the fenestra ovalis. This is corroborated by a stapes *in situ* on one of the specimens of *A. gracilis* and by a displaced stapes with its distal end still near the stapedial recess in a specimen of *A. casei.*

The stapedial recess is very distinct; a pronounced ridge, dorsal to the medial portion of the quadrate condyle, forms its ventro-medial border. It is extremely probable that there was a tympanic membrane in *Araeoscelis*, attached in the manner described by Romer and Price (1940, p. 62) for the pelycosaurian membrane: ". . . below the surface in a vertical plane at right angles to the . . . stapes and . . . diagonal to the long axis of the skull . . . the anterior margin of the drum attached to the

quadrate along a line passing downward internal to the quadrate foramen. . . ." The line "internal to the quadrate foramen" is a well-defined entity in the AMNH 4685 skull of *Araeoscelis*. Since the dorsal limit of this line lies near the ventrolateral corner of the paroccipital process, this corner probably represents the dorsal limit of anterior attachment of the tympanic membrane. The ventral limit of anterior attachment probably lay on the quadrate shortly below the stapedial recess. The posterior attachment of the tympanic membrane cannot be determined from the fossil materials; probably, as in lizards, this portion of the membrane's circumference was attached to muscular tissue and associated ligaments.

The lateralmost portion of the stapes was unossified; the appearance of the distal surface of the ossified part of the stapes shows that it must have been continued in cartilage. A large part of this cartilage was probably attached to the quadrate in the stapedial recess; this cartilaginous process would represent the quadrate process of the hyomandibular. Another cartilaginous process was attached to what we may, with confidence, call Schrapnell's membrane; this process is the tympanic process of the hyomandibular. The condition described is closely similar to that in *Captorhinus* where Parrington (1946a) found two distal surfaces on the stapes, one for quadrate articulation and one a ventral boss which must have been connected, either directly or via a short cartilaginous extension, to the tympanic membrane.

I have already described a small protuberance on the ventral border of the stapes near the stapedial foramen. This protuberance may possibly have served as a place of attachment for a ligament comparable to that which passed from the ventral surface of the pelycosaurian stapes. I doubt that such a ligament represents the ceratohyal connection; if it did, the stapedial-ceratohyal connection would lie medial to the stapedial-quadrate junction.

I have already noted the presence, on the posterior surface of the quadrate, of a broadly depressed area which runs from the stapedial recess to the paraquadrate foramen. The significance of this concavity will now become clear:

The M. depressor mandibulae must have been small in theropsids. Watson (1948) restored it as exceedingly slender in *Dimetrodon.*

When the mouth of *Araeoscelis* was closed, the retroarticular "process" projected posteriorly for only a very short distance. (*Araeoscelis* had no distinct retroarticular process as such.) Because of the convexity of the hind border of the cheek, the depressor mandibulae could not have taken origin very far dorsally; its origin probably covered a vertically elongate area from the ventral tip of the tabular to somewhere above the paraquadrate foramen. The muscle took origin from tabular, squamosal and quadrate. The posterior view of the articular shows that the insertion, as might have been expected from the area of origin and from the position of Schapnell's membrane, was limited mostly to the lateral part of the bone, the only part which is really retroarticular. If the muscle be reconstructed between origin and insertion, it will at once be seen that a vertically elongate, but appreciably wide slit is left between the muscle and the ventral portion of the posterior margin of the cheek. This slit was not closed by the bulging belly of the contracted muscle; rather, when the jaw was opened, the area of the slit was increased.

This slit lies lateral and slightly posterior to the depressed area between stapedial recess and paraquadrate foramen. I suggest that an external auditory meatus passed laterally from Schrapnell's membrane to run along the concavity in the quadrate and emerge between the M. depressor mandibulae and the quadratojugal portion of the cheek.

There is no difficulty in visualizing the course of the chorda tympani as it made its way, posterior to the tympanic cavity, to run along the medial surface of the mandible.

The account of the middle ear of *Araeoscelis* is that of the middle ear of an early theropsid reptile.

NON-OTIC COMPARISONS WITH THEROPSIDS VS. SAUROPSIDS

The evidences for early reptilian dichotomy are good; the architecture of the middle ear seems certainly to be a diagnostic key to this dichotomy. On the basis of this key, *Araeoscelis* can easily be seen as theropsid. Watson (1954) agrees with this assignation — for the same reason.

Are there further reasons for believing *Araeoscelis* to be a theropsid reptile?

Goodrich's evidences are useless in this respect. The structure

of the heart will certainly not help; the build of the fifth metatarsal, as I shall show, would be a dangerous criterion in this case.

We need to distinguish between 1) habitus features (in the sense of Gregory) and 2) those features which are clearly a legacy from a distant ancestor and which are not the result of recent adaptive trends. Among the latter features, we must differentiate between a) those characters of theropsids which are primitive — in the sense of inheritance from the common ancestry of theropsids and sauropsids — and b) those anatomical marks which are probably peculiar to theropsids.

The salient diagnostic features of the genus *Araeoscelis* lie in supratemporal fenestra, cervical vertebrae, teeth and pes. The structure of these parts, I believe, must be thought of as part of the animal's habitus. Other features of the *Araeoscelis* skull which we must consider under habitus are the prefrontal ridge, the coronoid process of the mandible, and the fact that the level of jaw articulation is considerably ventral to the level of the maxillary tooth row.

The supratemporal fenestra was undoubtedly concerned with more efficient muscular action. The main origin of the temporal muscle in this region was most likely by tendinous attachment to the periphery of the fenestra while fleshy fibers probably arose directly from a spanning ligament (cf. Case 1924). With the bulk of the muscle originating peripherally, there was space between bundles to accommodate its bulge when contracted. The habitus feature here is not the position of the muscle — probably primitive — but its mechanically advantageous fenestral origin.

The low level of jaw articulation made for better leverage, allowing the jaws to close in a more powerful bite.

The coronoid process of the mandible presented a broad surface for temporal muscle attachment, filled in a gap which would otherwise have existed between the jaws due to the low level of jaw articulation, and may also be considered as a response of the bone to the pull of powerful muscles.

The prefrontal ridge can only have served as protection for the orbital region.

The pattern of the teeth must obviously be an adaptation to diet. The sharp, peg-like anterior teeth, the lack of any teeth suited for crushing work, and the generally graceful build of

the skeleton which indicates an animal of active habits all suggest a carnivorous, perhaps insectivorous, diet. The apparently rapid mode of tooth replacement would render invalid any speculation based on the lack of abrasive wear on the transversely widened teeth. I do not believe it possible to be more specific; all small Permian reptiles need not have subsisted on cockroaches.

The elongate cervical vertebrae are probably also an adaptation to feeding habits. What habits, I cannot say.

I shall speak of the hind foot later.

The above features cannot be used in the determination of relationships between large groups. That *Lanthanosuchus* (Efremov 1946), with "synapsid" temporal openings, is regarded by Romer (personal communication 1953) as a possible procolophonoid and that *Bolosaurus*, with the same sort of openings, is regarded by Watson (1954) as essentially a cotylosaur and a sauropsid at that are strong supports for my opinion that the supratemporal fenestra of *Araeoscelis* need not be phylogenetically connected with the similarly situated fenestra of diapsids and lizards.

Stripped of its immediately adaptive features, what heritage characters remain in the skull to betray any theropsid connections of *Araeoscelis?*

It is well known that contacts between bony elements tend to be rather conservative in evolution. There are many obvious examples: the frontal-nasal contact, frontal-parietal contact, etc. Further, the absence of particular elements or the presence of neomorphs can often provide phylogenetic clues.

Except for the lack of an intertemporal, *Araeoscelis* has a full, labyrinthodont set of skull bones. The primitive contacts are all present — or nearly so.

A supratemporal-postorbital contact is considered primitive. With the loss — or coalescence with another bone — of the intertemporal, such a contact was inevitable. This contact is present in *Limnoscelis* (Romer 1946) and in pelycosaurs (Romer and Price 1940). *Diadectes* may have retained an intertemporal (Olson 1947); Olson (1950) has shown that the supratemporal and intertemporal of *Diadectes* may fuse, producing a compound element which is in contact with the postorbital (cf., however, criticism in Watson 1951, 1954).

The early supratemporal-postorbital contact of reptiles was

quickly lost. Among theropsids, the contact had already disappeared in the captorhinomorph line, e.g., in *Captorhinus* (Price's fig. in Romer 1945), *Protorothyris* and *Romeria* (Price 1937); *Labidosaurus* (Williston 1925) lacked the supratemporal altogether. Among sauropsids, the supratemporal-postorbital contact may have persisted into *Youngina*. (Restorations vary; cf., e.g., Parrington 1937 and Romer 1946.) Procolophonids, e.g., *Procolophon* (Watson 1914b) and *Nyctiphruretus* (Efremov 1940), lacked the supratemporal.

In *Araeoscelis,* the ventral end of the supratemporal just misses touching the posterior arm of the postorbital below the supratemporal fenestra. In terms of strict contact between these particular elements, the condition in *Araeoscelis* would have to be regarded as less primitive than that in *Limnoscelis* and pelycosaurs but more primitive than the condition in *Captorhinus, Romeria, Protorothyris* and *Labidosaurus.* However, the situation is complicated by the supratemporal fenestra whose presence may well be responsible for the lack of contact. *Araeoscelis* may be considered as possessing, in essence, the primitive supratemporal-postorbital contact.

Araeoscelis has paired postparietals, a primitive character. Paired postparietals are present in *Captorhinus, Protorothyris,* and *Romeria* (Watson 1954). *Limnoscelis* (Romer 1946) seems to have a median, unpaired postparietal, unexpected in this otherwise primitive form, but Romer (personal communication 1954) thinks the sutures in this general region in *Limnoscelis* to be too indistinct to allow any positive statement. *Youngina* has been interpreted as having (e.g., Parrington 1937), and as not having (Romer 1946) paired postparietals; in any event, the probable relationship of *Seymouria* to *Diadectes* would make paired postparietals primitive for sauropsids.

Tabulars are present in *Araeoscelis* as they are in *Limnoscelis* (Romer 1946), *Protorothyris, Paracaptorhinus* and other captorhinomorphs (Watson 1954). Again, *Youngina* is variously interpreted. Olson (1950) found the tabulars more or less distinct in some specimens of *Diadectes.* Tabulars are present in *Procolophon* (Watson 1914b), *Nyctiphruretus* and *Nycteroleter* (Efremov 1940).

The supratemporal, postparietal and tabular of *Araeoscelis* have primitive contacts with their neighboring elements; this

point is considered in detail under the sections on the respective bones.

We might perhaps say that the location of the tabulars in *Araeoscelis* — on the occipital surface — is a theropsid character. In the early sauropsids which retain this bone, it is a dorsal, as against a more strictly occipital, element; this is probably due to otic notch expansion, as opposed to closure. The position of the tabular in *Diadectes, Nyctiphruretus* and *Nycteroleter* corroborates this view. If Parrington's restoration of the tabular of *Youngina* be accepted, the location of the element in this genus fits in with the described sauropsid plan. In captorhinomorphs, on the other hand, the tabulars are distinctly occipital bones; this is clearly the situation in *Limnoscelis* (Romer 1946) and in those captorhinids (Watson 1954) which retained the tabulars. Pelycosaurs (Romer and Price 1940) have definitely limited their tabulars to the occipital surface.

The occipital plate of *Araeoscelis* is roughly similar to that of pelycosaurs. The occipital plates of both can easily be seen as derived from the *Limnoscelis* stage. There is, however, considerable variation among the theropsids in this region; in *Captorhinus* (Watson 1954), the posttemporal fenestrae are greatly enlarged, the paraoccipital processes are slender, and the supraoccipital has been appreciably narrowed.

Are there any postcranial marks of theropsid connections?

The vertebrae are of the typical cotylosaurian style — modified, however, by lateral excavation of the neural arch, and, in the cervical region, by elongation. They are primitive; it is as easy to see them as similar to those of *Nyctiphruretus* (Efremov 1940) as it is to see their resemblance to those of *Captorhinus* (personal observation). There is nothing unique about *Araeoscelis* in the abrupt decrease in transverse interzygapophyseal distance in the first sacral vertebra; this condition is found in *Seymouria* (White 1939), lizards and *Captorhinus* (personal observation) among others — but not in pelycosaurs (cf. Romer and Price 1940, pl. 25).

The possible presence of a tail break mechanism in *Araeoscelis* need not be a sign of sauropsid affinities; Price (1940) reported a similar mechanism in *Captorhinus*, a form which Watson (1951, 1953) regards as undoubtedly theropsid.

The pattern of rib articulation seen in *Araeoscelis* can be easily

derived from the primitive mode as seen in, e.g., *Seymouria* (White 1939). I was, at one time, struck by the close resemblance between varanid lizards and *Araeoscelis* in the articulation of the anterior dorsal ribs. This resemblance is heightened by the absence in *Araeoscelis* of intercentral articulation of the capitulum. The fact that the Squamata are suspected of having lost the tuberculum (Williston 1925) seemed significant in the face of the evidence that the posterior dorsal ribs of *Araeoscelis* have only a capitular articulation. Serial homology can, however, be dangerous.

Diadectes has holocephalous ribs (holocephalous in the sense of Williston 1925 — as distinct from morphologically single-headed) which articulate continuously from the intercentral space to the arch (Williston 1925). Ophiacodonts may be considered as having holocephalous ribs too although the thin web of bone between capitular and tubercular areas marks them as already dichocephalous (Romer and Price 1940). The anterior dorsal ribs of *Araeoscelis* may be regarded as holocephalous in the sense that this term may be used for ophiacodonts. The lack of intercentral articulation in *Araeoscelis* may be due to the small size of the intercentra. If the loss of tubercula from the ribs of the Squamata be a fact, and if this condition be compared with the loss of tubercular attachment in the posterior dorsals of *Araeoscelis*, the comparison is probably not much more significant than that between *Araeoscelis* and the domestic cat — whose posterior dorsal ribs also lack tubercular attachment. I cannot see that the ribs of *Araeoscelis* can be used as positive evidence for either theropsid or sauropsid connections. I shall return to this subject of ribs in discussing the affinities of *Araeoscelis* with the Protorosauria.

There has been some confusion on the systematic worth of the presence of a posterior coracoid. In labyrinthodonts, excepting *Seymouria*, there is but one ossification in the endochondral girdle (Romer 1947b). In *Seymouria* (White 1939) the scapula and a coracoid element — probably the anterior coracoid — ossify separately. *Diadectes* has but a single coracoid (fig. in Romer 1945), but pareiasaurs (Boonstra 1932) have two coracoids. The structure and history of the two coracoids in pelycosaurs and therapsids are well known (cf. Romer 1945). *Limnoscelis* has two coracoids (Williston 1911), and J. B. Clark (personal com-

munication 1953) is of the opinion, from his studies on *Protorothyris,* that two coracoids were the rule in all typical captorhinomorphs — a fact sometimes obscured by fusion.

"It is generally, and probably correctly, assumed that but one [coracoid] element was present in the ancestral reptiles and a second element added only by the forms antecedent to the mammals. . . . But there are some elements of doubt in the story of the coracoids. . . ." (Romer 1948, p. 116). I do not see why the posterior coracoid's presence need be significant in terms of broad phylogeny; as with the sternum, it may be a case of a cartilaginous element's becoming ossified in some forms but not in others. In lizards (Romer 1922), ligaments perform functions, e.g., providing a place of origin for the coracoid head of the M. triceps, taken care of by the posterior coracoid in pelycosaurs. There is no reason why lizards could not have been derived, with reduction in ossification, from a form with two coracoids.

Parrington (1953) considered the two coracoids of *Aenigmasaurus* to be sufficient reason for refusing this animal diapsid assignation. Mostly on the basis of the same evidence, he thought *Aenigmasaurus* to be a late survivor of an extremely primitive captorhinomorph-synapsid stock. Parrington suggested — with great reservation — a possibility that the paired sternal plates seen in some diapsids might be homologous with the posterior coracoids of synapsids. The presence in the lower Permian *Araeoscelis* of a well-ossified sternum plus two coracoids certainly does not lend any support to Parrington's suggestion.

The presence of two coracoids is not sufficient reason to assign *Araeoscelis* to the theropsids. The very close resemblance of the posterior coracoid of *Araeoscelis* to that of pelycosaurs, even to the process for the coracoid head of the M. triceps, might, however, be noted.

I do not regard the slim, lizard-like build of the humerus of *Araeoscelis* as phylogenetically significant. The proportions of limb elements are, as pointed out by Romer and Price (1940), associated with the absolute bulk of the animals concerned; (p. 137) ". . . the limb bones of large pelycosaurs appear to be short and broad as contrasted with related smaller forms . . . there has been no decrease at all in proportionate length; the differences lie entirely in the breadth of the elements."

Araeoscelis has both ectepicondylar and entepicondylar hu-

meral foramina. *Sphenodon* has both foramina. Lizards have the ectepicondylar foramen. *Captorhinus* has an entepicondylar foramen. In all pelycosaurs, the entepicondylar foramen is well developed, and both foramina are found in *Edaphosaurus* (Romer and Price 1940). Since a combination of the two foramina occurs in examples of both sauropsids and theropsids, no broad phylogenetic significance is attached to the presence of the two foramina in *Araeoscelis.* It is worth noting that Romer and Price (p. 140) found an ectepicondylar foramen in the humerus of an *Eryops*-like rhachitome.

The elongate anterior epipodials are probably correlated, as in *Petrolacosaurus* (Peabody 1952), with rapid locomotion. I cannot see that their morphology is indicative of either theropsid or sauropsid affinities.

The manus is no key here. All the primitive reptilian elements are present. The elongation of the preaxial centrale is similar to the condition in *Petrolacosaurus.* The large size of the fourth metacarpal is an exaggeration of a condition found in both theropsids, e.g., *Varanops* (Romer and Price 1940), and sauropsids, e.g., *Nyctiphruretus* (Efremov 1940).

The pelvis is as much like that of ophiacodonts as it is lizard-like — allowing for a lesser degree of ossification in lizards. A few points on comparison of pelvic muscular attachments between *Araeoscelis* and pelycosaurs were presented under the section on the pelvis.

The femur of *Araeoscelis* is no more easily compared with that of lizards — which it resembles — than it is with that of *Captorhinus* or of a small pelycosaur such as *Mycterosaurus* (Romer and Price 1940, fig. 37). Again, light build is associated with small absolute size.

The light build of the posterior epipodials, as of the anterior epipodials, is probably associated with rapid locomotion.

The structure of the pes might seem, at first, to bar *Araeoscelis* from theropsid relationship. Both in *Araeoscelis* and in typical terrestrial sauropsids, e.g., lizards, there is a locked tibio-astragalar joint, there is a mesotarsal articulation, and the fifth metatarsal is widely divergent from the other metatarsals. The varanid lizards (personal observation, Harvard specimens) might be thought to show remarkably detailed resemblance to *Araeoscelis* in the nature of the tibio-astragalar joint; in both, there is

a ledge of the medial (ventral) surface of the astragalus which receives a projection of the distal end of the tibia. This medial ledge serves to strengthen the main, proximal part of the joint. The medial and proximal portions of the articular surface of the astragalus are quite distinct in *Araeoscelis;* in *Varanus,* they are smoothly confluent. There is considerable variation among lizards; in *Iguana,* the proximal articulatory surface of the astragalus faces more laterally (dorsally) than it does medially, and no portion of the joint lies on the medial surface. The similarity in detail between the joints of *Araeoscelis* and *Varanus* is best regarded as a matter of convergence.

The primitive tibio-astragalar joint (cf. Schaeffer 1941, fig. 1) was neither a lateral (dorsal), rolling one as in pelycosaurs and *Captorhinus* nor is there any evidence that it was a locked one as in lizards and in *Araeoscelis.* There was no sign of any shift of articulation to either the lateral or the medial surface of the "astragalar" region.

The tibio-astragalar joint of the early sauropsid *Diadectes* (fig. in Romer 1944) was definitely proximo-lateral and probably admitted of some movement (Schaeffer 1941). We cannot, from Efremov's (1940) figures of the pedes of *Nyctiphruretus* and *Nycteroleter,* decide as to whether or not the joint was locked; the tibio-astragalar joint of the pes assigned (with some doubt) to *Nycteroleter* could not, however, have been lateral as in *Diadectes.* There was apparently some variation among early sauropsids in the nature of this articulation.

The pelycosaurian tibio-astragalar joint (figs. in Romer and Price 1940) was obviously movable, leading to the functional, cruro-tarsal articulation of mammals. The lateral, rounded tibial surface of the astragalus of *Captorhinus* (cf. fig. in Peabody 1951) denotes a movable cruro-tarsal articulation for this animal too.

There is good reason to believe, however, that a movable cruro-tarsal articulation was not universal among captorhinomorphs. The hind foot of *Limnoscelis* (Williston 1911, fig. 7) seems to be not far removed from the primitive pattern. There is an element present in the proximal tarsal row which can be interpreted only as a separate and distinct intermedium. Romer (1946) felt that the presence of this intermedium in the pes of *Limnoscelis,* no tibiale being present, substantiated his view, of the time, that

the reptilian astragalus was derived wholly from the labyrinthodont intermedium. The work of Peabody (1951) has shown, however, that the astragalus must have originated by combination of the intermedium, tibiale and fourth centrale. Undoubtedly, as Schaeffer (1941) suspected, a tibiale — ossified or cartilaginous — was present in *Limnoscelis.* The large distal surface of the tibia bears this out. Schaeffer considered the tarsus of *Limnoscelis* as almost identical with that of *Seymouria.*

Schaeffer's conclusion that there was very little movement between tibia and astragalus in *Labidosaurus* and that (p. 430) ". . . there is reason to believe that the functional ankle-joint was still in its old location between the tarsalia and the metatarsals" would seem to indicate that the evolution of the tibio-astragalar joint within the Captorhinomorpha proceeded in two directions: 1) to a functional cruro-tarsal ankle-joint and 2) to a locked joint between tibia and astragalus.

The origin of reptiles must be sought deep below the Permian; the Pennsylvanian *Petrolacosaurus* (Peabody 1952) is already a highly developed terrestrial form. It is not inconceivable that, with increasing ossification in the early reptiles, the locked tibio-astragalar joint might have begun its development almost at the outset of the history of the reptiles.

In view of the indifferent character of the tibio-astragalar joint in *Limnoscelis,* and in view of the occurrence among both theropsids and sauropsids of both mobility and locking at this joint, I cannot consider the locked joint in *Araeoscelis* to be evidence for the animal's belonging to either group. If anything at all is to be made of the joint, it is simply that those early theropsids with a functional cruro-tarsal articulation were nearer the line to mammals than were other theropsids.

I do not consider the functional mesotarsal joint of *Araeoscelis* as indicative of either sauropsid or theropsid relationship. This joint is probably part of the same habitus as are the locked tibio-astragalar joint and the divergent fifth metatarsal. Schaeffer (1941) decided that the mesotarsal joint was not functional in the Eosuchia. The functional ankle-joint in *Youngina* was not, however, a cruro-tarsal one; on the contrary (p. 437), "The nature of the articular surfaces at this point would seem to indicate greatly restricted movement in a dorso-plantar direction, if indeed, there was any movement at all. The principal

plane of flexure must have been tarsometatarsal in position." Broom's (1921, 1924) figures of the *Youngina* tarsus show that the shallowly concave, proximomedial tibial surface of the astragalus must have held the tibia in a firm lock. Indeed, the appearance of the tibial and fibular surfaces of the *Youngina* astragalus bear a remarkable similarity to the lizard condition. If the eosuchians are truly ancestral to the rest of the Lepidosauria and to the Archosauria, then it is significant that *Araeoscelis,* in the Lower Permian, had developed a movable mesotarsal articulation before that condition had arisen in the Eosuchia — as exemplified by the Upper Permian *Youngina.* This may be considered as evidence for the independent derivation of the functional mesotarsal joint of *Araeoscelis.*

Aside, Gregory (1945, p. 312) felt that *Trilophosaurus* had a ". . . typically sauropsidan intratarsal joint. . . ." but he also thought (p. 315) that "Considerable motion, particularly rotation, was possible between tibia and astragalus. This surface [of the astragalus], however, is flat." This would give the animal a combination of mesotarsal and cruro-tarsal articulations. Dr. J. T. Gregory has kindly lent me some materials of *Trilophosaurus* — including tibia, calcaneum, cuboid and fifth metatarsal. Dr. J. A. Wilson has generously had an excellent cast of the astragalus prepared for me. In addition, I have had access to a very good cast, in the collection of the Museum of Comparative Zoology, of the dorsal surface of the *Trilophosaurus* pes.

The distal end of the *Trilophosaurus* tibia is definitely unsuited for articulation with the flat surface on the lateral (dorsal) face of the astragalus. I suggest that the tibia did not articulate with the dorsal surface of the astragalus, but that, instead, the joint occurred on the proximoventral surface. (Both surfaces are pictured in plate 30 of Gregory's paper.) Study of the *Trilophosaurus* astragalus reveals that this proximoventral surface would receive the tibia in a curved, possibly immovable joint which has some resemblance to the corresponding joint in lizards. A tuberous portion of the tibia, probably for muscular attachment, would then project medially and ventrally from the tibioastragalar joint — as in *Araeoscelis.*

I thought, for a while, that the cuboid bone of *Trilophosaurus* might easily be seen as derived, by reduction, from the cuboid of *Araeoscelis.* Actually, certain theropsid developments show

far more similarity to the *Araeoscelis* condition. If the fourth and fifth distal tarsals of *Captorhinus* (Peabody 1951, fig. 2) had been coalesced, a cuboid like that of *Araeoscelis,* tapering to an acute postaxial end and receiving the fifth metatarsal on its postaxial-distal surface, would have resulted. The postaxial portion of the *Araeoscelis* cuboid, unlike the corresponding portion of the *Captorhinus* "cuboid," is free of calcaneal contact. It is not, however, among sauropsids that we see a condition similar to this detail in *Araeoscelis;* it is in the gorgonopsid *Lycaenops.* (Schaeffer 1941, Colbert 1948; Schaeffer's figure has the tarsus articulated in a manner which more closely illustrates this point.)

Araeoscelis apparently led the life of a Permian "lizard." The divergent fifth metatarsal is a part of this habitus. It must be noted that there is no similarity in detail; the fifth metatarsal of *Araeoscelis* is not hooked. However, even though Goodrich (1942) attempted to show that the fifth metatarsal of *Youngina* was hooked, it was certainly not obviously so, and it must be assumed that the hook probably arose *within* the Lepidosauria.

That the Chelonia exhibit the hook is an argument against any necessity of *Araeoscelis*-sauropsid affinities. Since *Youngina* has either no hook at all or only an incipient one, and since all other known eosuchians do have it (Schaeffer 1941), it probably arose within the Eosuchia. We must suppose, therefore, either that the turtles arose from the eosuchians or that the chelonian hook is an independent development. I am sure that most students of turtles would prefer the latter alternative. If we admit that the hooked fifth metatarsal arose at least twice among the sauropsids, it then seems quite possible that the nature of the *Araeoscelis* fifth metatarsal — which is, after all, only divergent and not at all hooked — is an independent development.

Perusal of the figures of pelycosaurian pedes (Romer and Price 1940, fig. 41) will immediately show that, in these undoubted theropsids, a strongly divergent fifth metatarsal was by no means uncommon.

Certain dissimilarities in detail of the lizard pes as compared to that of *Araeoscelis* — reduction or loss of fifth distal tarsal, loss of centrale, more or less complete fusion of astragalus and calcaneum — are obviously not significant.

To sum up, *Araeoscelis* had a pes much like that of a lizard,

but no phylogenetic connection need be assumed.

In this discussion of the non-otic structures of *Araeoscelis*, we have found no features which can be confidently used in a broad phylogenetic assignation of the genus. Except, perhaps, for some close resemblance between *Araeoscelis* and pelycosaurs in the build of the pectoral girdle, the non-otic similarities to theropsids can be considered as due to primitiveness. The non-primitive features in which *Araeoscelis* resembles the sauropsids can readily be seen as matters of habitus. We must use some feature in *Araeoscelis* which is neither a habitus feature not a feature inherited, in common with all reptiles, from its remote ancestry. Such features are to be found in the architecture of the middle ear. Even though the build of the fifth metatarsal is probably not the key to sauropsid identification Goodrich thought it to be, the other evidences for reptilian dichotomy are sound. The structure of the truncus arteriosus is significant, Watson's thesis of the otic notch as a key character seems to work, and the evidences of the chorda tympani and tympanic membranes have been shown to support Watson's basic ideas.

It is interesting that the otic region may be an especially reliable character within the mammals. What are the key osteological distinctions between marsupials and placentals? Prepubic bones, inflected mandibular angle, palatine fenestrae, and the structure of the auditory region seem to be the only good ones. Prepubic bones are unossified in thylacines. *Tarsipes* lacks an inflected mandibular angle, and the palatine fenestrae are not universally present in marsupials (Flower 1885) ; the structure of the auditory region is the only really reliable key. The tympanic bone in marsupials is small, simple and loosely attached —may, indeed, be lost in dry specimens — and the major protection offered the floor of the tympanic cavity is by a posterior wing of the alisphenoid which may, as it does in *Phascolarctos*, even form a bulla-like structure (Flower 1885). Were prepubic bones, palatine fenestrae and inflected mandibular angle absent in a fossil marsupial, the structure of the animal's ear alone would be sufficient to betray its relationship.

When it is considered that the basic dichotomy of reptiles is intimately associated with differential otic development, it will be readily appreciated that the structure of the middle ear is an

even more important key character among reptiles than it is among mammals.

The structure of its middle ear marks *Araeoscelis* as theropsid. We have, in *Araeoscelis,* what may be called a "theropsid lizard." In view of its habitus — lizard-like pes, general gracefulness of build — we may suppose that this animal helped fill an ecological niche, in the Lower Permian, similar to the niche now filled by lizards.

COMPARISONS WITH PROTOROSAURS

Though Huxley (1871) set up the group Protorosauria with *Protorosaurus* as type genus, the term has, since Williston's (1910, 1914) description of *Araeoscelis*, come to be generally accepted as the designation for an order built around the latter genus (Romer 1947a). It is necessary, in the light of the here presented evidence of its theropsid nature, to reëxamine the question of relationship between *Araeoscelis* and the genera with which it has been ordinally grouped. This is especially desirable in view of Camp's opinion that *Protorosaurus* is an eosuchian (Camp 1945).

Romer (e.g., 1945) recognized a subclass Synaptosauria made up of the orders Protorosauria and Sauropterygia and characterized by the diagnostic features: 1) a supratemporal fenestra and 2) a tendency toward a single-headed dorsal rib articulating with the transverse process of the neural arch rather than with the centrum.

Similarity in temporal fenestral pattern need not be indicative of relationship. *Lanthanosuchus* and *Bolosaurus* have lower temporal fenestrae but are not synapsids. Diapsids have, in addition to a lower temporal fenestra, a supratemporal fenestra; yet Romer (1945) felt that protorosaurs and eosuchians were not closely related. A corollary of Romer's view is that the supratemporal fenestrae of *Araeoscelis* and of lizards are not phylogenetically connected. On the matter of rib similarities, I have shown that it is the tuberculum, not the capitulum, which is lost in the posterior dorsal ribs of *Araeoscelis.* I see no tendency in *Araeoscelis* toward dorsal ribs articulated, as in sauropterygians, high up with a transverse process of the neural arch alone.

The assignation of plesiosaurs to their proper side of the

basic reptilian dichotomy is a very difficult task and one which I am not qualified to undertake. Placodonts (cf. figs. 161, 162 in Romer 1945), supposed relatives of the plesiosaurs, show a sauropsid-like otic notch; perhaps otic notch reduction took place in plesiosaurs in response to an aquatic environment's having made bone conduction of sound possible. I cannot, of course, rule out the possibility of the derivation of sauropterygians from some line of araeosceloids; there may have been a major shift in rib articulation. Again, it is not certain that the ribs of *Araeoscelis* did not articulate with a downgrowth over the centrum of the neural arch; especially is this uncertain of the cervical ribs. But, even though this uncertainty exists, there remains the fact that the evolution to sauropterygians must have included a shifting upward of the dorsal rib articulation. It is the upward shift which is important here; such a shift need not have been dependent on the rib's having previously been completely articulated with the neural arch rather than partly with the centrum nor is it necessary to suppose that articulation wholly with the neural arch must presage such a shift. The significant fact is that there is no observable tendency toward an upward shift in dorsal rib articulation in *Araeoscelis;* rather, the serial loss of the tuberculum would seem to indicate an emphasis on central — at least functionally central — articulation. I feel that, in the absence of more convincing evidence and intermediate forms, there is nothing to be gained by classifying *Araeoscelis* with the sauropterygians.

Romer (1945, p. 191): "Where sufficiently known, . . . [the protorosaurs] show certain basic features described in *Araeoscelis* — a single, upper, temporal opening; slim, single-headed cervical ribs; and dorsal ribs in which the two heads tend to unite to a single one situated on or close to the transverse process." The arguments against *Araeoscelis*' placement in the Synaptosauria on the basis of dorsal ribs and temporal openings may be used here too, against *Araeoscelis's* placement with the other forms commonly considered as "protorosaurs." As to the cervical ribs of *Araeoscelis*, I have shown that at least the posterior of these are holocephalous (again, in the sense of Williston) rather than truly single-headed.

The order Protorosauria has always been a "trash basket;" very few of the genera assigned to this group are seen as cer-

tainly allied, one to another. Since we are concerned with the degree of relationship of each of these genera to *Araeoscelis,* it will be best to compare *Araeoscelis* with each in turn. There has already been much discussion on the connections of *Araeoscelis* with its supposed protorosaurian relatives (bibliography in Romer 1947a). The unfortunate fact is that most of these animals are poorly known. Actually, the diagnostic features which I have already indicated as unsafe criteria for the placement of *Araeoscelis* in the group — character of temporal fenestra and ribs — are about the only marks which have held the protorosaurs together as a systematic unit. In appreciation of the extensive literature — mostly inconclusive — on the subject of protorosaur interrelationships, it would be futile to attempt to rework the matter here. I shall restrict myself to comparisons I consider pertinent, e.g., Is the genus under consideration theropsid or sauropsid? Is there any reason at all for banding the genus with *Araeoscelis?*

The listing of the protorosaurian genera follows that of Romer (1945). Citations are to the more important discussions, not necessarily to the original descriptions.

Araeoscelis and *Ophiodeirus* are synonyms.

Kadaliosaurus (Credner 1889) of the German Rothliegende is known from the better part of its postcranial skeleton, but no skull has been found. Williston (1914) studied the materials and was convinced of the animal's close relationship to *Araeoscelis.* Romer (1947a) stated that the *Kadaliosaurus* humerus is identical with that of *Araeoscelis.* From Credner's figure, I must agree that the two genera look remarkably alike. Williston felt that the two forms ought to be kept in separate genera due to the presence of cancellous tissue in the long bones of *Kadaliosaurus* where these bones in *Araeoscelis* are hollow. I might add that the tibia of *Kadaliosaurus* seems to be appreciably more robust than that of *Araeoscelis.* Williston's advice ought to be followed, at least until *Kadaliosaurus* is better known. It is interesting that a well developed armature of ventral ribs was present in *Kadaliosaurus;* this indicates that such a system might have been present in *Araeoscelis* too. It must be remembered that most of the really diagnostic features for comparison with *Araeoscelis* — temporal fenestra, teeth, ear, cervical vertebrae — are not available for inspection in *Kadaliosaurus.* The pes is in-

complete, but the tibio-astragalar joint seems definitely to be a locked one. Though the legend accompanying Credner's plate states that the abbreviations "fi" and "ti" were interchanged in lithography, the tibia and fibula are, in fact, correctly labeled. The labels for astragalus and calcaneum were interchanged, however.

Broomia (Watson 1914) of the South African Middle Permian is known from a palatal view of its skull and a fair amount of postcranial material. The cervical vertebrae and pelvic girdle are not known. The carpus and tarsus were well preserved. *Broomia* resembles *Araeoscelis* in slender proportions but this may be, as Romer (1947a) has suggested, merely a function of small size. *Broomia* and *Araeoscelis* are similar in the serial pattern of their maxillary teeth: anterior conical teeth grading posteriorly into a file of transversely widened teeth which, in turn, give way posteriorly to conical teeth. Very dissimilar to the conditions in *Araeoscelis* are the following features of *Broomia*: The basisphenoid is very broad and is not hidden from ventral view by the parasphenoid. The basipterygoid processes are directed so that their articular surfaces lie at a right angle to the long axis of the skull. The ventral border of the cheek seems to be emarginated — as in lizards and in nothosaurs. The articular region of the quadrate lies far in advance of the basioccipital — as in *Milleretta* (Broom 1938). There is no posterior coracoid. There are no signs of distal humeral foramina. The carpus has three centralia, the postaxial one between ulnare and fourth distal carpal. The fourth metacarpal is not more robust than the third.

It would be dangerous to ally *Broomia* and *Araeoscelis;* their resemblance lies in the fact that they are both small reptiles. It is interesting here that Broom (1938, p. 541) thought ". . . the palate of *Broomia* resembles so closely that of *Millerina* [*Milleretta*] that one can hardly avoid the conclusion that the two genera must be related." We shall have occasion to return to *Milleretta*.

Aphelosaurus (Gervais 1858) of the French Permian was perhaps best taken care of by Watson (1914c, p. 1008) when he said: "The animal is, in fact, so incompletely known that little can be said about it." Watson's opinion did not change with the years, and lately (1954, p. 435) he declared *Aphelosaurus*

"incapable of discussion." From what I can make of the animal (Thevenin 1910, fig. 29, pl. 7), its similarity to *Araeoscelis* lies in its elongated limbs. The tibiae of the two genera are not alike; that of *Aphelosaurus* is far too broad distally. The tarsus is unlike that of *Araeoscelis;* the astragalus and calcaneum seem to be very simply formed and there are at least four small distal tarsalia — with probably a fifth. The fourth metacarpal of *Aphelosaurus* is no larger than its third. The animal is too poorly known for speculation. It would be unwise to place it in a group with *Araeoscelis*. Peyer (1937) assigned *Aphelosaurus* to the Protorosauria, but Peyer was thinking in terms of *Protorosaurus* and *Macrocnemus*.

Adelosaurus of the English Upper Permian was founded by Watson (1914c) on materials earlier assigned (by Hancock and Howes 1870) to *Protorosaurus* as *Protorosaurus huxleyi*. There is no resemblance to *Araeoscelis*. The extremities of the humerus are only slightly expanded, the pisiform almost equals the ulnare in size, there is no fifth distal carpal, and the fourth metacarpal is not much larger than the third. There is but a single coracoid. The affinities of this genus must remain obscure until better materials are known.

Protorosaurus of the German Kupferschiefer was described by Spener in 1710. Von Meyer founded the genus in 1830 and the species, *P. speneri,* in 1832. Seeley (1888) reviewed the early history of the genus; references to the early literature will be found in his paper. Von Meyer (1856) published descriptions and illustrations of most of the materials. Seeley (1888) described the type skeleton — which von Meyer had not seen — and presented a reconstruction. Huene (1926) restudied *Protorosaurus* and produced a new restoration. Weigelt (1930a, 1932) published photographs of some new fragments and (1930a) set up *Gracilisaurus ottoi* as a new genus and species, the diagnostic difference from *Protorosaurus* lying in the former's supposed phalangeal formula, ?-3-3-3-3, for its manus. Romer (1947a) suggested that *G. ottoi* might be a young specimen of *Protorosaurus* and that the tips of the third and fourth digits might have been lost with the unpreserved counter-slab.

The skull of *Protorosaurus* is poorly known; especially is this true of the temporal region. Since the present paper's contributions to the cranial anatomy of *Araeoscelis* have mainly to do

with the structure of the temporal region, I can, unfortunately, add little to the comparison of the skulls of the two genera.

Camp (1945) saw the skull of *Protorosaurus* as very closely similar to that of *Prolacerta*. Due to the nature of the materials, this opinion was based mostly on general outlines and proportions. Romer (1947a), answering Camp, showed that, in most of the features Camp used to compare *Protorosaurus* and *Prolacerta*, *Araeoscelis* is as like *Protorosaurus* as is *Prolacerta*. Only in the fact that the teeth of both *Protorosaurus* and *Prolacerta* are sharp, single-pointed and slightly recurved can these two genera be positively seen as more closely similar to one another in skull structure than *Protorosaurus* is to *Araeoscelis*.

Camp thought the cervical vertebrae and cervical ribs of *Prolacerta* to be much like those of *Protorosaurus* — as, indeed, they are. The neural spines are highly developed in the cervical vertebrae of both genera; the ribs are splint-like and articulate by two heads which are only slightly separated from one another. Romer answered that the cervical vertebrae of *Protorosaurus* are more elongate than those of *Prolacerta* and thus resemble more closely the situation in *Araeoscelis*. I do not consider elongation of cervical vertebrae to be a good phylogenetic key; *Macrocnemus* (Peyer 1937), assigned to the Protorosauria, has cervical vertebrae very little more elongate than those of *Prolacerta*.

From what I can make of von Meyer's figures and Seeley's reconstruction, there seems, in *Protorosaurus*, to be a rather rapid transition from the low, ventral attachment of the cervical ribs to the high attachment of the dorsal ribs. There is a very smooth transition between the cervical and the dorsal modes of rib articulation in *Araeoscelis*. Huene (1926) thought the transition in *Protorosaurus* to be more gradual than pictured by Seeley, but I cannot see the widely separated heads of the cervical ribs of Huene's restoration to be at all consonant with the figures given by von Meyer. Even if Huene's reconstruction were to be accepted, the fact remains that the ribs of *Araeoscelis* do not, passing posteriorly, shift as far dorsally as do those of *Protorosaurus* (and *Tanystropheus*, where the shift occurs in one leap). Further, only in the portion of the column posterior to the region of cervical-dorsal transition are the ribs of *Araeoscelis* truly bicipital.

The chevrons of *Araeoscelis* are not distally expanded as are those of *Protorosaurus,* but this is a minor difference.

Huene figured the shoulder girdle of *Protorosaurus* with two coracoids in 1926 but later (1944a) drew it with only one coracoid — the apparently correct interpretation. It is not at all like that of *Araeoscelis.*

The details as to humeral foramina in *Protorosaurus* are not clear; both Camp and Romer were uncertain on this point.

I cannot see any similarity between the manus of *Araeoscelis* and that of *Protorosaurus;* comparison of von Meyer's figures with the figure of the *Araeoscelis* manus in this paper will make this immediately obvious.

The fifth metatarsal of *Protorosaurus* is definitely hooked; this hooking acts to bring the fifth into a line parallel with the other metatarsals. The pes of *Protorosaurus* resembles more the typical sauropsid type than it does that of *Araeoscelis.*

I see no difficulty in allying *Protorosaurus* with forms like *Macrocnemus* and *Tanystropheus,* but I cannot see it as related to *Araeoscelis.* I am inclined to accept Camp's (1945) suggestion that *Protorosaurus* is related to the eosuchians, and I believe that certain points to be discussed in relation to *Macrocnemus* and *Tanystropheus* will lend support to this idea.

Eifelosaurus (Jaekel 1904) of the European Lower Triassic is known from parts of its postcranial skeleton only. It has a fairly elongate femur, but any similarity to *Araeoscelis* ends there. The dorsal ribs of *Eifelosaurus* attach to strong diapophyses, the second sacral rib is large and distally bifurcate, and the anterior caudal ribs are not recurved. In its costal articulation, *Eifelosaurus* shows relationship to *Tanystropheus* and company, but there is no reason to assume any connection with *Araeoscelis.*

Microcnemus (Huene 1940) of the Lower Triassic of Northern Russia is known from a fair amount of postcranial material and a probably correctly referred skull fragment — consisting of parts of the upper and lower jaws. The dentition is acrodont. The coronoid process of the mandible rises as a narrow projection above the general coronoid region. Except that the costal articulatory surfaces on the vertebrae demonstrate that the cervical ribs were truly bicipital — with the tuberculum a short

distance dorsal to a capitulum articulating far ventrally on the centrum — the cervical vertebrae are somewhat similar to those of *Araeoscelis.* A vertebra which Huene took to be from the region of cervical-dorsal transition seems to show that the transition from cervical to dorsal rib articulation was a smooth one. The dorsal ribs were articulated near the anterior end of the centrum and were not attached to high transverse processes. The costal facets of the caudal vertebrae are situated further dorsally — on a level with the vertebral foramen — than are the corresponding facets in *Araeoscelis.*

The humerus of *Microcnemus* was not well preserved. The build of the femur is generally similar to that of *Araeoscelis.*

Huene pictured a scapulocoracoid which he felt belonged to *Microcnemus* although he expressed some slight doubt as to the association. There is no distinctly triangular supraglenoid buttress, there is no process for the coracoid head of the M. triceps, and the coracoid terminates shortly behind the glenoid region. The glenoid cavity is, however, screw-shaped. Only one coracoid is indicated by suture, but this is a rather long element when compared with most anterior coracoids. The ischium bears no resemblance to that of *Araeoscelis.*

While it is by no means inconceivable that *Microcnemus* may be a modified early Triassic survivor of the araeosceloid stock of "theropsid lizards," the differences in dentition and scapulocoracoid would, in view of the lack of better cranial materials, make any such assignation an unjustified one. The mode of cervical rib articulation is reminiscent of that in *Protorosaurus,* and the slender appearance of the cervical vertebrae may be correlated with the animal's habitus — including small size.

Trachelosaurus (Broili and Fischer 1917) is known from some girdle and limb elements but mostly from its vertebrae and ribs; no skull is known. Broili and Fischer, describing what they thought to be a reptile with some twenty cervical vertebrae, assigned *Trachelosaurus* to the Sauropterygia. The build of the ilium, however, seemed to them to be that of a terrestrial reptile, and so they felt *Trachelosaurus* should be considered as representative of a special group of sauropterygians. Huene (1944c) carefully analyzed the plate given by Broili and Fischer and came to the conclusion that the figured slab contains the remains

of more than one individual and that, therefore, the cervical vertebral count is nowhere near as great as the original describers thought it to be. Huene assigned *Trachelosaurus* to the Protorosauria.

Neither the cervical vertebrae nor the cervical ribs bear any resemblance to those of *Araeoscelis*. The neural arch of *Araeoscelis* is more low-slung, and its spine shows none of the corrugation seen on the neural spines of both the cervical and dorsal vertebrae of *Trachelosaurus*. The dorsal ribs of *Trachelosaurus* are attached to stout transverse processes from the neural arches. I see no reason for allying *Trachelosaurus* with *Araeoscelis*, but the former's mode of dorsal rib articulation might reasonably qualify it for admission to the *Tanystropheus* camp of protorosaurs.

Macrocnemus (Peyer 1937) of the Alpine Middle Triassic is known from a crushed skull and fairly numerous postcranial parts. As Peyer has figured the skull, *Macrocnemus* shows some resemblance to *Prolacerta* in a possibly streptostylic quadrate. The build of the squamosal of *Macrocnemus* certainly suggests a lower temporal fenestra — possibly lacking, as in lizards, a ventral osseous border. The poor state of preservation of the temporal region forbids further comparison. The general shape of the anterior portion of the skull is similar to that of *Protorosaurus* and *Prolacerta*, but, as pointed out by Romer (1947a), the shape of this region in *Araeoscelis* is hardly different. *Macrocnemus* has *Protorosaurus-Prolacerta* type teeth.

The cervical vertebrae are moderately elongate with fairly well developed neural spines; these spines have each a long, longitudinal ridge along the dorsal border. The neural spines of *Protorosaurus* have no such ridge and tend to an antero-posterior subdivision. The cervical ribs of *Macrocnemus* are quite long. Peyer supposed certain two-headed ribs in the material to belong to the region of cervical-dorsal transition; most of the dorsal ribs are single-headed — as in *Tanystropheus*. Inspection of Peyer's figures will show that the dorsal ribs of *Macrocnemus* articulated high up, on the neural arch.

There is but one coracoid, and the shoulder girdle is, in a general way, of a lepidosaurian-like build. The pelvis has a thyroid fenestra. Anterior and posterior limb elements are elon-

gate. The carpus is not well preserved, but the tarsus is; the tibio-astragalar articulation was a proximal — as opposed to dorsal — one. The three preaxial distal tarsalia have been reduced to leave but one small element. The fifth metatarsal is distinctly hooked and articulates proximal to the other metatarsals. The fourth metacarpal and fourth metatarsal are larger than the respective third metapodials; this is not the situation in *Tanystropheus*.

Peyer's analysis has established *Macrocnemus* as a relative of *Protorosaurus* and *Tanystropheus*. The manner of dorsal rib articulation and, especially, the probably lepidosaurian character of the skulls of *Macrocnemus* and *Tanystropheus* remove these genera from kinship with *Araeoscelis*. A comparison of rib articulations in *Araeoscelis* and *Macrocnemus* would indicate that the dorsal ribs of *Macrocnemus* have lost their capitula; this is significant inasmuch as the tendency in *Araeoscelis* was, at least serially, towards reduction of the tuberculum.

Tanystropheus[1] (Peyer 1931) of the Alpine Middle Triassic is known from poorly preserved cranial materials and, with the exception of the shoulder girdle, an almost complete, though composite, set of postcranial bones. In view of the nature of the remains, Peyer did not attempt detailed analysis of the temporal region although he did detect a supratemporal fenestra. Working with better materials, Kuhn (1947) was able to make the following observations: 1) There are two temporal fenestrae; the bottom one is open ventrally. 2) The quadrate is streptostylic. 3) The palate is kinetic. Kuhn came to the conclusion that *Tanystropheus* is a lepidosaur and suggested that the genus has no relation to *Araeoscelis*. Dr. Kuhn was kind enough to write to me in 1951 and reiterate his opinion that "*Tanystropheus* ist ein hochspezialisierter Lepidosaurier."

Tanystropheus is famous for its enormously elongate cervical vertebrae and neck. Due to their drastic modification, it is difficult to compare the structure of these vertebrae with those of more conservative genera. The cervical ribs are extremely long and are, with the exception of the twelfth, single-headed. Every

[1] There has been much confusion in the nomenclatorial history of this genus; among other things, the correct name is apparently *Macroscelosaurus* Münster (cf. Broili 1915), not to be confused with the Karroo reptile *Macroscelosaurus* Haughton. It is certainly best to continue, as Peyer has done, with the familiar term *Tanystropheus*.

dorsal rib is single-headed and articulates with a transverse process from the neural arch. The shift from the cervical to the dorsal mode of rib articulation is startlingly abrupt; while the last cervical rib is attached to a far ventral part of the anterior end of the centrum, the first dorsal rib articulates high up, on the neural arch, at a point about midway in the vertebra's length. I consider the picture of costal articulation in *Tanystropheus* to represent the extreme of a tendency found in all those reptiles which we may call, at this point, the "euprotorosaurs."

The shoulder girdle of *Tanystropheus* is unknown; the pelvis has a large thyroid fenestra. The pro- and epipodials are elongate. The carpus and tarsus seem to demonstrate reduction in ossification. Though Peyer did not, in 1931, figure the fifth metatarsal as at all hooked, he did, in the reconstruction, indicate that it articulated proximal to the other metatarsals. In 1937, comparing *Macrocnemus* and *Tanystropheus,* Peyer drew a slightly revised figure, picturing the fifth metatarsal as somewhat hooked.

I am inclined to agree with Kuhn as to the lepidosaurian affinities of *Tanystropheus.*

Zanclodon of the European Middle Triassic was first described by Plieninger (1846) from remains of teeth and dorsal vertebrae. Huene (1931) discussed various isolated finds of cervical and dorsal vertebrae from the Lower Muschelkalk. Most of the cervical vertebrae show some similarity to those of *Tanystropheus;* there are some resemblances to those of *Araeoscelis,* but one can easily distinguish between the two. Unfortunately, the manner of cervical costal articulation is not known. Huene felt that the dorsal vertebrae which he had described were very similar to those of *Zanclodon* — and they are. Except for some differences in proportions, the dorsal vertebrae of *Zanclodon* resemble very much those of *Tanystropheus.* On the basis of possible association — generic or specific, not individual — of the *Tanystropheus*-like cervical vertebrae and the *Zanclodon*-like dorsal vertebrae, Huene suggested that *Zanclodon* might be considered a species of *Tanystropheus.* The teeth of *Zanclodon* are recurved, sharp, and have serrate edges; they are unlike those of *Araeoscelis* but may be favorably compared with a general *Protorosaurus-Macrocnemus* pattern. The dorsal ribs, not known, must have been single-headed; the dorsal vertebrae each bear an obvi-

ous transverse process from the neural arch. This transverse process lies, as in *Tanystropheus,* about midway along the vertebra's length.

If the cervical and dorsal vertebrae figured by Huene do belong to a single genus or species, we have an animal obviously related to *Tanystropheus* but apparently, as Romer (1947a) has commented, less specialized. In any event, the animal described as *Zanclodon* by Plieninger shows no sign of connection to *Araeoscelis.*

Trilophosaurus (Gregory 1945) of the Texas Upper Triassic is known in almost its complete bony anatomy. The skull, with its large otic notch, immediately betrays this genus as sauropsid. In many lizards, e.g., *Iguana, Lacerta,* the quadrate is shallowly depressed laterally so that the tympanic cavity extends anteriorly between the tympanic membrane and the lateral surface of the quadrate. This arrangement permits the quadrate to assume a structurally stronger shape without the necessity of diminution of the area of the tympanic membrane. The lateral surface of the *Trilophosaurus* quadrate is shallowly recessed from the general lateral surface of the skull; this recess tapers anteriorly so that the anterior border of the quadrate lies flush with the lateral surface of the squamosal. The build of the quadrate thus indicates that the tympanic cavity extended anteriorly between quadrate and tympanic membrane, that the tympanic membrane was quite large, and that the membrane was attached along a line anterior to the posterior border of the quadrate, possibly near the squamosal's hind edge. There exists, in some lacertilians, e.g., *Conolophus,* a distinct notch in the posterior border of the quadrate where the columella passes behind this bone to reach the tympanic membrane; in some mosasaurs (cf. Zittel 1890, figs. 546, 547) this notch is closed posteriorly, forming a stapedial meatus. The posterior border of the *Trilophosaurus* quadrate is gently concave; this concavity is most pronounced near the upper portion of the border. Presumably, as in lizards (cf. Versluys 1899, Goodrich 1930), the columella of *Trilophosaurus* — known only from its proximal portion — was inserted into the tympanic membrane at a point considerably dorsal to the membrane's center. The whole quadrate has a generally sauropsid appearance. Gregory thought that because the quadrate of *Trilophosaurus* curves backward over the otic notch, the

notches of *Trilophosaurus* and *Diadectes* showed only superficial similarity, but later observations (Romer 1946, Olson 1947) have shown that the quadrate curves backward over the notch in *Diadectes* too. Gregory, throughout his paper, expressed his conviction of the sauropsid nature of *Trilophosaurus;* of the braincase, he said (p. 287) : "The enclosed, dorsally placed inner ear and small fenestra ovalis and rod-like stapes are advanced features characteristic of the Sauropsida generally (in contrast to the Therapsida)."

Beyond the presence of supratemporal fenestrae in both genera, there is no similarity between the skulls of *Araeoscelis* and *Trilophosaurus.* The fenestrae are not alike in the two genera, that of *Trilophosaurus* separated from its partner of the other side by a thin sagittal crest.

Both the cervical and dorsal vertebrae of *Trilophosaurus* have well developed neural spines. The cervical ribs, except for those of the atlas and axis, are bicipital and are possibly fused to the transverse processes. The first four dorsal ribs are bicipital and show, serially, a gradual shift dorsally of the parapophyseal-capitular joint. The fifth dorsal rib is attached wholly to the diapophysis which, in *Trilophosaurus,* is an outgrowth from the neural arch at the level of the vertebral foramen. While the diapophysis of this vertebra has a special facet—continuous with the main diapophyseal facet — for articulation with the capitular portion of the rib, the succeeding diapophyses, passing posteriorly, gradually do away with this facet, and, by the eleventh dorsal vertebra, the rib articulation has lost all signs of double-headedness. Serially then, while the ribs are functionally single-headed from the fifth dorsal vertebra on, the indications are that this single-headedness is the result of fusion of capitulum and tuberculum. In any event, the sequence is similar to the familiar "euprotorosaurian" story: the dorsal ribs, reading from anterior to posterior, shift dorsally to articulate with a single transverse process from the neural arch midway in the length of the vertebra.

Trilophosaurus has but one coracoid and no trace of a screw-shaped glenoid cavity.

In Gregory's own words (p. 306) : "The details of the humerus suggest that *Trilophosaurus* is more closely related to the Lepidosauria than to other groups." The femur is elongate, but I do

not see in it the striking similarity to *Araeoscelis* that Gregory saw.

I find no similarity between the carpi of *Araeoscelis* and *Trilophosaurus.* I have already discussed in this paper the probably inflexible tibio-astragalar joint of *Trilophosaurus.* Gregory thought that both cruro-tarsal and intra-tarsal joints were functional in *Trilophosaurus;* I believe that only the latter was functional. The pes is of a typically sauropsidan pattern.

I agree with Gregory on the sauropsid, probably lepidosaurian affinities of *Trilophosaurus* and should, as he did, group it with the protorosaurs — but I cannot see it as allied with the araeosceloids. Dr. Gregory was, of course, unaware of the theropsid nature of the *Araeoscelis* ear.

Weigeltisaurus (=*Palaeochamaeleo,* nom. praeocc., cf. Kuhn 1939) of the German Kupferschiefer is known from skull, limbs, some vertebrae, and some girdle scraps. Weigelt (1930b) published photographs and a description of the materials. The skull, of a shape and ornamentation reminiscent of that of *Chamaeleo,* is apparently equipped with both upper and lower temporal fenestrae. The photographs do not permit an analysis of the otic region. The dentition is acrodont. There seem to be no cervical vertebrae among the remains. The fairly elongate dorsal vertebrae were not well preserved, but the few known dorsal ribs are single-headed. The shoulder girdle is not known; the pelvic girdle was very poorly preserved. The pro- and epipodials are elongate. The carpal elements cannot be clearly made out, and the tarsus is beyond discussion. The build of the fifth metatarsal cannot be ascertained. Weigelt considered the genus to be lepidosaurian.

Coelurosauravus (Piveteau 1926) from the Permian of Madagascar is known from a few cranial scraps and scattered postcranial parts. Huene (1930) pointed out that what is known of this genus indicates clearly that the animal is very closely related to, if not congeneric with, *Weigeltisaurus.* Both Huene and Watson (letter quoted by Huene) felt that the denticulated bones which Piveteau described as mandibles ought really to be interpreted as part of a frill like that on the skull of a chameleon — and on the skull of *Weigeltisaurus.* The preserved elements of *Coelurosauravus* do resemble those of *Weigeltisaurus,* but, even if the two are closely related, there is very little in the

materials of the former which can add to our knowledge of these forms' anatomy.

Before reviewing the relationships of the protorosaurian genera, it will be best to briefly discuss two recently described reptiles.

Aenigmasaurus (Parrington 1953) from the Lower Triassic of South Africa is known from dorsal vertebrae, some ribs, the girdles, propodials and parts of the epipodials. The costal facets of the dorsal vertebrae show that there was a gradual transition from the cervical to the dorsal mode of rib articulation, but it is not known how many vetebrae lay in the transitional region. The first two preserved dorsal vertebrae are equipped with both parapophysis and diapophysis. The third preserved dorsal vertebra has only a diapophysis — which has, however, an anteroventral extension. Unfortunately, the second preserved vertebra is poorly known in its parapophyseal region, and so the method of transition is not perfectly understood. It would seem, however, that the capitulum, passing posteriorly, shifted dorsally to unite with the tuberculum. From the third preserved dorsal vertebra posteriorly, the costal attachment is solely diapophyseal. Although there is some close resemblance between the anterior dorsal vertebrae of *Aenigmasaurus* and those of *Araeoscelis* — the manner of rib articulation is similar and the ribs, themselves, are somewhat alike — there are also some differenees; the vertebrae of *Aenigmasaurus* are not notochordal, they have no mammillary processes, and the neural arches are not laterally excavated. The chief difference between the vertebral columns of the two genera lies in the serial change in costal articulation; although the diapophysis does not, in *Aenigmasaurus,* shift to a very high position, it is the diapophysis which remains and the parapophysis which is lost. This is the reverse of the serial change seen in *Araeoscelis.* Both the first and the second sacral vertebrae have distally expanded transverse processes in *Aenigmasaurus* — very unlike the condition in *Araeoscelis.* There is another point of dissimilarity in that the decrease in transverse interzygapophyseal distance occurs in the second sacral vertebra of *Aenigmasaurus;* in *Araeoscelis,* this decrease occurs in the first saeral. The costal processes of the *Aenigmasaurus* caudal vertebrae are outgrowths of the neural arches, quite unlike the picture in *Araeoscelis.*

Aenigmasaurus has two coracoids, the anterior one excluded from the glenoid cavity. The *Aenigmasaurus* pelvis is primitive except for a strengthening anterior ridge of the ilium.

Except for the absence of an entepicondylar humeral foramen, the anterior and posterior propodials of *Aenigmasaurus* are roughly similar to those of *Araeoscelis,* but, as pointed out elsewhere in this paper, such similarities may well be correlated with absolute bulk.

Parrington analyzed *Aenigmasaurus* rather carefully and came to the view (p. 734) that this genus has ". . . a skeleton which, except in its shoulder-girdle, bears remarkable resemblance to those of the early diapsids." This opinion was based on critical study of the remains of *Youngina* and *Palaeagama.* The presence of two coracoids in *Aenigmasaurus* brought Parrington to conclude (p. 737) that the genus was ". . . a very late survivor of extremely primitive captorhinomorph-synapsid stock." On this basis, Parrington thought the theory of captorhinomorph origin of the diapsids to be strengthened. I take exception to this conclusion. Watson's theories on reptilian dichotomy do not depend on coracoidal structures. Procolophonids and pareiasaurs, groups which Watson assigned to the sauropsids, have both anterior and posterior coracoids. Further, as Parrington himself indicated (p. 733), "Little can be said of the shoulder-girdle of *Youngina* and *Palaeagama* since they are very imperfectly preserved." Romer (1948) cautioned against the casual acceptance of the thesis that a second coracoid was added only by forms antecedent to mammals; he warned (p. 116) that ". . . there are some elements of doubt in the story of the coracoids. . . ."

Much of Parrington's problem arose from the fact that (p. 735) ". . . Watson (1951) has objected to the interpretation of the middle ear of captorhinomorph and synapsid reptiles advanced by Westoll and supported by [Parrington]. . . ." I have shown, however, that the theories of Parrington, Watson and Westoll are, with modifications, consonant.

In my scheme, *Aenigmasaurus* is a sauropsid, possibly a lepidosaur, possibly a "euprotorosaur."

Petrolacosaurus (Peabody 1952) from the Upper Pennsylvanian of Kansas is known from a fragmentary skull with a good palate, from its axial column, and from its limbs. Peabody

has recently obtained several new specimens including skull materials, but since no published account of these new finds has yet appeared, this discussion will be based on the 1952 description.

Peabody thought the appearance of the borders of the badly preserved squamosal and jugal to indicate the presence of a lower temporal fenestra. On the basis of his views on the possible eosuchian affinities of *Petrolacosaurus,* he restored the skull — with much misgiving — as diapsid. The palate of *Petrolacosaurus* is plainly dissimilar to that of *Araeoscelis* in the former's possession of a broad, plate-like parasphenoid and in the presence of a row of teeth on this bone's presphenoidal rostrum. The teeth of *Petrolacosaurus* are simple, roughly conical, and show no sign of labyrinthine structure. Watson (1954) has analyzed the skull, especially the quadrate region, and considers the genus theropsid.

The atlas of *Petrolacosaurus* differs from that of *Araeoscelis* in that the latter's atlantal centrum has fused with the axial intercentrum. The axes of the two genera are much alike in shape of neural spine and in the position of the facets for the atlantal neural arch. The cervical vertebrae of the two genera differ in that those of *Petrolacosaurus* have high neural spines and are not elongated. *Petrolacosaurus'* cervical and dorsal ribs are, in essence, dichocephalic, but the capitulum of each is attached to the tuberculum by a thin web of bone. Peabody's (p. 20) "Measurements of capitular-tubercular separation, when compared with the articulatory ridge on the vertebra, indicate that the capitulum of all precaudal ribs, except the posterior dorsals, articulated with the intercentrum or close to it. A small posterior dorsal rib . . . has a head too small . . . to extend beyond the diapophyseal ridge." Again, this is the reverse of the serial transition seen in *Araeoscelis.*

The coracoids of *Petrolacosaurus* are unknown. On the basis of his new finds, Peabody has announced that the pelvis figured in his paper had been incorrectly referred and is not of *Petrolacosaurus;* an accurate description is forthcoming.

Anterior and posterior pro- and epipodials are thin and elongate, but the propodials are not as gracefully constructed as are those of *Araeoscelis.* The humerus has a primitive appearance, its extremities finished in cartilage. There is an entepicondylar foramen.

The carpi of *Petrolacosaurus* and *Araeoscelis* are very much alike in the build of radiale, ulnare and fourth distal carpal, and, especially, in the elongation of the preaxial centrale. The calcaneum of *Petrolacosaurus* lacks the postaxial expansion seen in *Araeoscelis*. The tibial facet of the *Petrolacosaurus* astragalus is concave and is directed proximally and preaxially; it is not the dorsal, rounded facet of the pelycosaurian cruro-tarsal joint. The distal border of the astragalus bears a distinct notch. Peabody analyzed the tibio-astragalar articulation as a positive, inflexible one and suggested that the functional joint was mesotarsal. All these characters of the astragalus agree closely with the condition in *Araeoscelis*. Some differences exist. The vertical neck of the *Petrolacosaurus* astragalus is distinct in its elongation. The ventral shelf for accessory tibial articulation — which assures so positive a lock in *Araeoscelis* — is lacking in *Petrolacosaurus*. The rest of the pedal elements, including fifth metatarsal, are not unlike in the two genera; the fourth and fifth distal tarsalia of *Petrolacosaurus* are more primitive in their individuality. Peabody thought the first distal tarsal to have been absent. I suspect that it was lost in preservation, that the postaxial shift of the first three digits (Peabody, fig. 9) is, as Peabody recognized was the case for the fourth and fifth digits, a postmortem displacement, and that the digits were placed, with respect to the distal tarsalia, much as in *Araeoscelis*.

Peabody placed great emphasis on the supposed dissimilarity between *Araeoscelis* and *Petrolacosaurus* in their carpi and tarsi. In this he was misled by Williston who had erroneously identified an isolated tarsus of *Araeoscelis* as a carpus.

I have mentioned that Watson considers *Petrolacosaurus* to be theropsid; I am inclined to agree with him. *Araeoscelis* and *Petrolacosaurus* differ in rib articulation, but then, so does *Araeoscelis* differ from many pelycosaurs in this respect. I have, in this paper, stressed the character of costal articulations mainly in order to show that this feature cannot well be used, as it has been, to tie *Araeoscelis* in with the "euprotorosaurs." As to temporal openings, Peabody has himself said (p. 34) that ". . . it must be granted that the evolution of post-orbital fenestrae in reptiles passed through a stage or stages, possibly in the Pennsylvanian, when 'extra openings' were of questionable taxonomic value." The autopodia of *Araeoscelis* and *Petrolacosaurus* show

great resemblance to one another, and, remembering that *Petrolacosaurus* is the geologically older animal and understandably more primitive in limb structure, the one may be seen as possibly derived from the other. It may be that the two genera are related; further speculation is best deferred until after the appearance of a more complete description of the skull of *Petrolacosaurus*.

The views expressed in this paper on *Araeoscelis*-protorosaur interrelationships may be summed up at this point.

The pattern of temporal fenestration seen in *Araeoscelis* is not evidence enough to band this genus with forms like *Tanystropheus* and *Trilophosaurus*. Neither can the mode of costal articulation be used for such a grouping. The capitulum of the dorsal rib does not lose its articulation with the centrum in *Araeoscelis;* rather, it is the tuberculum which is lost serially. The "euprotorosaurian" tendency is for the capitulum to shift dorsally and unite with the tuberculum in a diapophyseal attachment typically midway in the length of the vertebra. Such a pattern is clearly evident in *Trilophosaurus* and reaches its extreme expression in *Tanystropheus* where the shift occurs in one step, the capitulum possibly dropping out altogether. I do not contend that some protorosaurs might not have varied from this typical pattern.

How do the costal articulations in *Araeoscelis* compare with those in other theropsids? We may refer to the best known group of early theropsids — the pelycosaurs. Passing posteriorly in the pelycosaurian vertebral column, the capitulum and tuberculum come to be closely appressed (Romer and Price 1940). In some species, e.g., *Dimetrodon loomisi* (*op. cit.*, fig. 64), the appressed capitulum and tuberculum articulate, in the lumbar region, at a rather high level, and in other species, e.g., *Edaphosaurus pogonias* (*op. cit.*, fig. 68), the posteriormost dorsal ribs articulate at a level relatively no higher than do the corresponding ribs in *Araeoscelis*. But, in every case where the neurocentral suture can be made out in the posterior dorsal vertebrae of pelycosaurs, the single costal articulatory area is seen to be on both arch and centrum (*op cit.;* Romer, person. commun. 1954). As in the comparison with plesiosaurs, the matter is complicated by the lack, in *Araeoscelis*, of sutures to accurately distinguish arch from centrum. Here again, however, we may make an attempt at a functional com-

parison. Considered functionally, the terms parapophysis and diapophysis may reasonably be used here to denote, respectively, a place of attachment to the central region — be it morphologically wholly composed of centrum or not — and a place of attachment to the neural arch. Looked at in this way, *Araeoscelis* is seen, in the serial retention by its ribs of a parapophyseal articulation — i.e., in its emphasis on a functionally central costal articulation — to resemble the primitive pelycosaurs, e.g., *Ophiacodon* (cf. Romer and Price 1940, fig. 43). Looked at morphologically, *Araeoscelis,* in its serial loss of the tuberculum, is unlike either the ''euprotorosaurs'' or the pelycosaurs.

The serial shift dorsalward of the capitulum seen in *Araeoscelis* and pelycosaurs is not at all like that seen in *Trilophosaurus* and *Tanystropheus* in which genera the shift produces the typical dorsal rib. The shift in *Araeoscelis* and pelycosaurs is correlated with the posteriorward decrease in rib size. This is especially clearly seen in *Araeoscelis*: both the parapophyseal and diapophyseal facets decline in area passing posteriorly; the diapophysis keeps its dorsal position while the reduction in parapophyseal area takes place from below upward. Thus, what might at first look to be a dorsalward shift of the capitular attachment in *Araeoscelis* is, in reality, a dorsalward shift of only the ventral border of this attachment.

Light, graceful build of the limb bones is a feature which seems frequently to be stressed in the description of possible protorosaurs. Since this is a factor of absolute bulk, it cannot be used as an argument for tying *Araeoscelis* in with the Protorosauria. The scaloposaurids are a group of therocephalians which include some rather small forms with lightly built limbs. One of these forms, *Ericiolacerta* (Watson 1931) of the South African Lower Triassic, has a skull subequal in size to that of *Araeoscelis*. *Ericiolacerta* is well known and it is obvious that the animal is a therapsid. On the other hand, the skull of the probably related *Macroscelesaurus* (Haughton 1918) is poorly known. This reptile has slender limbs and might have been classified as another protorosaur; indeed, the very imperfect remains of the animal look superficially similar to many of the protorosaurian fossils. Fortunately, the few bits of skull which were preserved enabled Haughton to analyze the genus as therapsid.

Protorosaurus, according to Peyer and to Romer, is related

to *Macrocnemus* and *Tanystropheus.* In view of the lepidosaurian character of the skull of the last genus (Kuhn 1947) and in consideration of the probably streptostylic quadrate of *Macrocnemus* (Peyer 1937), it is not hard to agree with Camp (1945) on the lepidosaurian affinities of *Protorosaurus.*

Dr. Watson, in 1952, was kind enough to sketch the otic region of *Milleretta* for me. Apparently, Broom's (1938) reconstruction of this area is not quite correct; the millerettids seem to have a sauropsid otic notch. As I understand Dr. Watson, he feels that the eosuchians might well have been derived from among the millerettids. In this connection, the close resemblance between the palates of *Milleretta* and *Broomia* (cf. Broom 1938, p. 541) may prove to be significant with respect to *Broomia's* systematic placement.

Trachelosaurus may be related to *Tanystropheus; Zanclodon* probably is. *Coelurosauravus* and *Weigeltisaurus* are probably lepidosaurs of one sort or another. Unfortunately, many of the protorosaurs are so badly preserved that blanket statements are dangerous, but I should say that, with the exception of *Araeoscelis* and *Kadaliosaurus,* they may well, as Camp (1945) has suggested, be assigned to the Lepidosauria.

This addition would not startlingly increase the diversity of the Lepidosauria. As demonstrated by the obviously lepidosaurian *Askeptosaurus* (Kuhn 1952), some of these reptiles had already become considerably specialized by the Middle Triassic. The characteristic protorosaurian tendency in costal articulation is paralleled in the archosaurian descendants of the Lepidosauria; as Romer says (1945, p. 213): ". . . a common archosaurian feature is the tendency for the two heads [of the rib] to crowd closer together; in the cervical region the capitulum moves back to arise from the centrum below the transverse process, and in the trunk both heads may arise from the process itself."

It is not the concern of this paper to suggest how the "euprotorosaurs" ought to be arranged under Lepidosauria. I cannot, however, see the need for reterming, as Camp has advocated, the Eosuchia as the Protorosauria. Until more and better materials are available, it would seem wise to retain the two groups, Eosuchia and Protorosauria, as early subdivisions of the Lepidosauria.

THE PLACE OF ARAEOSCELIS AMONG THE THEROPSIDS

It still remains to consider the place of *Araeoscelis* among the theropsids.

Watson (1917) divided the Cotylosauria into Seymouriamorpha, Diadectomorpha and Captorhinomorpha. The seymouriamorphs, reptiles or not, are related to the diadectomorphs (Olson 1947, Watson 1951) and may be considered along with this latter group. We have then, in the Cotylosauria, a compromise between vertical and horizontal classification. The diadectomorphs are sauropsid cotylosaurs with exaggerated otic notches, and the captorhinomorphs are theropsid cotylosaurs with obliterated otic notches. Watson broke the Captorhinomorpha into Captorhinidae, Limnoscelidae and Pantylidae. Though reptilian relationship has been claimed for the microsaurs even quite recently (Westoll 1942a, 1942b), Romer (1950), surveying the group, came to the conclusion that microsaurs are neither reptiles nor ancestors of reptiles; accordingly, we may disregard the Pantylidae. J. B. Clark (personal communication 1953), a student of captorhinomorphs, would agree that the group ought to be split into limnosceloids and captorhinoids, but he feels that these subdivisions deserve higher rank than that of family; infraorders may be appropriate. Such an arrangement seems a sensible one, and we might compare it with Romer's (1945) breakdown of the Captorhinomorpha into families: The family Solenodonsauridae consists of forms questionably even reptilian (cf. Romer 1950) and need not be considered. Watson's work will demonstrate that the family Millerettidae is more closely related to diadectomorphs than it is to captorhinomorphs. The families Captorhinidae and Protorothyridae would be grouped together in the Captorhinoidea, and the family Limnoscelidae would be raised to Limnosceloidea.

To consider the placement of *Araeoscelis,* we must compare it with the early theropsid groups Limnosceloidea, Captorhinoidea and Pelycosauria.

Romer (1946, p. 169) came to the conclusions that "*Limnoscelis* appears to be a very primitive cotylosaur, the captorhinids very advanced forms" and that ". . . *Limnoscelis* is in almost every regard an ideal ancestor for the pelycosaurs and, through them, for therapsids and mammals. . . ." Finds of pelycosaurs in

the same beds with *Limnoscelis,* and the finds of *Petrolacosaurus,* probably older than *Limnoscelis,* demonstrate that this last animal was certainly not at the base of all theropsid evolution. As Romer (p. 186) analyzed the position of the genus, "*Limnoscelis,* despite its primitive character, was . . . a relict type, presumably a little modified descendant of the actual reptile ancestor of earlier Pennsylvanian days."

It is as representative of the structural type of the earliest theropsids that *Limnoscelis* may be profitably compared with *Araeoscelis.* As may pelycosaurs, so may *Araeoscelis* be easily seen as derived from a *Limnoscelis* stage. The skulls of *Araeoscelis* and *Limnoscelis* are alike in retention of the supratemporal-postorbital contact (essentially present in *Araeoscelis*) and the lacrimal-naris contact. Both genera have broad occipital plates. *Araeoscelis* is the more primitive in its retention of paired postparietals (But see discussion earlier in this paper.) and ought perhaps to be regarded as more primitive in its maxilla-quadratojugal contact, seen in so many anthracosaurs (cf. Romer, 1947b). *Araeoscelis* is advanced over *Limnoscelis* in the former's separation of prefrontal and postfrontal and in the reduction of the ventral arm of the tabular. Unfortunately, the stapes of *Limnoscelis* is not known, and the medial surface of the quadrate was poorly preserved.

Most of the changes from the *Limnoscelis* stage to *Araeoscelis* are changes in proportion. The *Araeoscelis* snout is anteriorly tapered in both dorsal and lateral views and has none of the massive build of the *Limnoscelis* snout. The skull of *Araeoscelis* is much less obviously triangular in dorsal view than is that of *Limnoscelis.* The occiput of *Araeoscelis* is higher and narrower.

The fenestra ovalis is similarly located in the two genera.

The teeth of *Limnoscelis* are labyrinthine; those of *Araeoscelis* are not. The shape of the teeth is considerably different in the two genera, those of *Limnoscelis* being of a more simple, primitive type with a minor specialization in the enlargement of the upper incisors.

The vertebrae of *Limnoscelis,* with swollen neural arches, are of the typical cotylosaurian type. With lateral excavation of the neural arch and elongation of the centrum, this sort of vertebra was probably ancestral to the *Araeoscelis* type. The ribs of *Limnoscelis* are holocephalous; Romer (1946, p. 177) states: "As

in primitive reptiles generally the articular area of the rib contracts in width in the more posterior part of the trunk, the capitular articulation shifting upward and backward from the intercentrum toward and to a point on the centrum below the transverse process.'' Such a condition was probably antecedent to the mode of costal articulation seen in *Araeoscelis*.

The shoulder girdle of *Limnoscelis* is, except for the presence of two coracoids, primitive. The pelvic girdle and anterior and posterior limbs are of the type expected in early reptiles with short, stout limbs.

That there is no barrier to the derivation of the pes of *Araeoscelis* from that of the *Limnoscelis* stage has already been discussed in this paper.

The ancestry of *Araeoscelis* may well lie near that of *Limnoscelis*.

As Romer has indicated, the typical captorhinoid genera *Captorhinus* and *Labidosaurus* are advanced and specialized in many features although *Protorothyris* and *Romeria* may be somewhat closer to *Limnoscelis*. Except for a few comparisons, discussion of the captorhinoids is best left to recent (Watson 1954) and forthcoming (Clark in MS) works which deal rather extensively with the group.

In *Protorothyris, Romeria* (Price 1937) and *Captorhinus* (Watson 1954) the supratemporal-postorbital contact has been lost. The supratemporal is very small in *Captorhinus* and apparently lacking altogether in *Labidosaurus* (Williston 1925). The occiput of *Captorhinus,* with its large posttemporal fenestrae and narrow supraoccipital, has departed much further from the *Limnoscelis* stage than has that of *Araeoscelis*. The multiple-rowed maxillary dentition of *Captorhinus* is a specialization. The recurved beak of *Captorhinus,* bearing enlarged incisors, is found also in *Romeria, Labidosaurus* and, incipiently, in *Limnoscelis* but not in *Protorothyris* or *Araeoscelis. Araeoscelis* resembles *Captorhinus* in the possession of paired postparietals, the two genera being both more primitive than *Limnoscelis* in this respect. *Araeoscelis* and *Captorhinus* both show advancement over the *Limnoscelis* stage in that their quadrates are directly supported by the paroccipital processes without the intervention of tabulars; *Araeoscelis* is, however, somewhat more primitive than *Captorhinus* in this respect since, in the former, the tabular

sends a thin arm to superficially cover the dorsalmost part of the contact between quadrate and paroccipital process.

The tarsus of *Limnoscelis* is primitive, almost identical with that of *Seymouria* (Schaeffer 1941). The tarsus of *Labidosaurus* is more advanced in that the proximal row of tarsalia has been reduced to two elements; it is, however, still primitive in its plane tibial surface and the fact that the functional ankle-joint was still tarso-metatarsal. The astragalus of *Captorhinus* (Peabody 1951, fig. 2) shows a cruro-tarsal joint of the pelycosaurian type.

Araeoscelis resembles the pelycosaurs in supratemporal-postorbital contact, broad occipital plate, and details of the shoulder girdle; differences in limb build are, as indicated by the structure of the smaller pelycosaurs, largely correlated with differences in absolute bulk. The universal pelycosaurian features of synapsid temporal fenestra and cruro-tarsal ankle joint make any direct ancestral connections unlikely, the similarities due probably to common descent and to general primitiveness.

The classification of Romer (1945) distributes the reptiles among six major systematic categories — subclasses. Two of these subclasses, the Anapsida and the Synapsida, contain theropsids, and a third, the Ichthyopterygia, may have been derived from among the theropsids (Romer 1948).

The pelycosaurs are a sufficiently distinct, numerous, and varied group to be removed from a common subclass with *Limnoscelis,* and their obvious relationship to the therapsids easily justifies their combination with this later group into the subclass Synapsida.

There are no such obvious connections for *Araeoscelis.* I can see no certain descendants. The sauropterygians, from a consideration of the placodont otic notch and from what Dr. Watson has told me of the plesiosaurian middle ear, are probably sauropsids. The ichthyosaurs are still dangerous area for speculation, and the mesosaurs will probably remain *incertae sedis* for some time to come. It is not improbable that *Araeoscelis* lost out in competition with lepidosaurian forms of similar habitus; the Upper Permian was full of small eosuchians. Replacement, in an ecological niche, of one systematic group by another is not uncommon. One of the most striking cases is that of the phytosaurs and crocodilians (Colbert 1949, p. 401): "The imitation

of the phytosaurian adaptive trend by the crocodilians is one of the most striking examples of parallelism to be seen in the fossil record. After the phytosaurs had become extinct, the crocodilians evolved in Jurassic and subsequent geologic periods to imitate almost completely the line of adaptive trend that had been followed earlier by the phytosaurs.''

Araeoscelis is an early theropsid bearing many primitive marks although specialized in various ways in its lizard-like habitus. *Araeoscelis* is not more different from *Limnoscelis* than is *Captorhinus*. Indeed, the latter's dentition, occiput, exceptionally large stapedial footplate, small supratemporal, and crurotarsal articulation qualify it as really more advanced than *Araeoscelis* although ''advancement'' leading to each of the two genera has proceeded along different lines of specialization.

The suborder Diadectomorpha is a highly varied group. *Bolosaurus* has a lower temporal fenestra. The millerettids possibly belong in this suborder. Some of the procolophonids were lizard-like forms; Efremov (1940) has so described *Nyctiphruretus*, and Colbert's (1946) restoration of *Hypsognathus* shows resemblance to *Phrynosoma* in habitus. As some of the procolophonids may be considered diadectomorph ''lizards,'' so, I feel, may *Araeoscelis* be considered a captorhinomorph ''lizard.''

It may, at first, seem strange to have ''apsid anapsids,'' but it hardly seems wise to make the presence and character of temporal fenestration the sole diagnostic criterion for assignation to subclass.

Williston (1913a) used the term Araeoscelidia to designate a suborder under which he placed *Araeoscelis* and *Kadaliosaurus;* he felt that Araeoscelidia ought to be considered as coördinate with Lacertilia and Ophidia under Squamata.

This term of Williston's is better used to designate an infraorder of the Cotylosauria with the following arrangement:

Subclass Anapsida

  Order Cotylosauria

    Suborder Captorhinomorpha

      Infraorder Limnosceloidea
      Infraorder Captorhinoidea
      Infraorder Araeoscelidia

Williston (1910) set up Araeoscelidae as the familial name but later (1912), in deference to the early date (1889) of Credner's description of *Kadaliosaurus,* used Kadaliosauridae. Since the name Araeoscelidae is the more familiar, and since it is taken from the better known genus, it seems better to retain Williston's earlier term.

Petrolacosaurus awaits more complete description, but it may be that this genus will become the type of another family of the Araeoscelidia.

Until genera certainly related to *Araeoscelis* are known, and until *Kadaliosaurus* is known from better specimens, there seems to be no purpose to any listing of diagnostic characters of genus and family; there are no differentials upon which to base such diagnoses.

The order Cotylosauria becomes more diversified with the addition of the Araeoscelidia. Future work may break the order into smaller packages. Such an undertaking is, however, beyond the scope of this paper, and I have placed *Araeoscelis* where I feel it most appropriately fits under a reasonably sound and orthodox scheme of classification.

SUMMARY

Study of the materials of *Ophiodeirus* Broom has shown this genus to be synonymous with *Araeoscelis* Williston; although there are no known osteological differences between the two, their different geological ages make retention of specific distinction desirable, *A. "Ophiodeirus" casei* occurring in the Wichita group and *A. gracilis* in the Clear Fork group of the Lower Permian of Texas.

Study of heretofore unworked materials of *A. casei*, restudy of Broom's specimens of *casei,* and restudy of the materials of *A. gracilis* have permitted a more complete and accurate description of the osteology of *Araeoscelis* than has previously been available. Fully treated for the first time are the palate, occiput and middle ear. It has been possible to round out our knowledge of the dermal skull roof, the dentition, the vertebrae, the serial changes in the mode of costal articulation, the pelvis, the propodials and the epipodials.

The possible existence of a tail-break mechanism and of sec-

ondary centers of ossification are discussed.

Of especial interest is the new description of the pectoral girdle; there is a single, screw-shaped glenoid cavity rather than the three separate glenoid facets previously thought to be present. There is an ossified sternum.

The earlier account of the manus is inaccurate and that of the pes is inadequate; both are redescribed, the latter at some length. The manus is, except for its elongate preaxial centrale, of a basically primitive reptilian pattern. The structure of the pes is rather lizard-like what with its locked tibio-astragalar articulation, the mesotarsal location of the functional ankle-joint, and the divergent — although not hooked — fifth metatarsal. Analysis of the mesotarsal and tarso-metatarsal joints suggests that *Araeoscelis* was essentially digitigrade.

It has been possible to determine sites of muscular origin and insertion on some of the postcranial elements. Such analysis indicates that some of the muscles attached fleshily in other reptiles were attached tendinously in *Araeoscelis*. This emphasis on tendinous attachment has permitted the determination of the place of origin of the Mm. ambiens and pubotibialis on a process of the pubis other than the lateral pubic tubercle, indicating that the main function of the tubercle was probably that of elevating the anteroventral anchoring place of the ilio-pubic ligament so that this ligament could, even in the absence of an anterior extension of the iliac blade, ride freely over the course of the M. puboischiofemoralis internus.

The Goodrich-Watson hypothesis of a basic dichotomy at the roots of reptilian phylogeny is discussed. Watson's thesis that the structure of the middle ear is evidence of this dichotomy and a key to the two resultant groups is supported by certain detailed relationships of the chorda tympani and tympanic membrane. Watson's idea that the theropsid reptiles altogether lacked a tympanic membrane is rejected; rather, the theories of Westoll on the homology of the amphibian tympanic membrane with the pars flaccida of the mammalian membrane seem, when combined with the basic propositions of Watson, to give a reasonable account of the evolution of the middle ear.

The chorda tympani of theropsid reptiles probably lay in its primitive position posteroventral to the original (labyrinthodont) tympanic diverticulum. In the later theropsids, a more

ventral diverticulum (recessus mandibularis of Westoll) probably pushed out ventral to the chorda tympani to end laterally, in the region of the angular, at the developing pars tensa. This would account for the presence of the chorda tympani in the posterior malleolar fold — between the partes tensa and flaccida — of the mammalian tympanic membrane.

During the process of otic notch expansion in the evolution to sauropsid reptiles, the chorda tympani was probably pulled anteriorly through a still thick tympanic "membrane" as a result of the removal of the hind end of the mandible to a more anterior position. Subsequent thinning of the membrane probably forced the nerve up against the posterior surface of the quadrate.

The middle ear of *Araeoscelis* is described in some detail and is seen to be that of a theropsid reptile. Evidence is presented for the existence, in *Araeoscelis*, of an external auditory meatus.

Araeoscelis is compared with theropsids and sauropsids in non-otic structures. *Araeoscelis* has, in many ways, a lizard-like habitus; this is especially so of the build of its pes. It is shown that such features are not necessarily indicative of phylogenetic relationship and that they are outweighed, in this respect, by the much more significant structure of the ear.

It is shown that the mode of costal articulation seen in *Araeoscelis* — with its serial loss of the tubercular attachment, i.e., in its emphasis on articulation with the (at least functional) centrum — militates against ideas of relationship to the sauropterygians.

Araeoscelis is compared with the individual protorosaurs, with *Petrolacosaurus,* and with *Aenigmasaurus.* The pattern of temporal fenestration — imperfectly known in many protorosaurs — is considered to be insufficient ground for the inclusion of *Araeoscelis* in the Protorosauria, and the pattern of costal articulation is seen to argue against such inclusion. The only likely connections seem to be with *Kadaliosaurus* and *Petrolacosaurus.* The protorosaurs, after the removal of *Araeoscelis* and *Kadaliosaurus,* may, following the suggestion of Camp, be assigned to a position near the eosuchians.

Araeoscelis is compared with cotylosaurs and pelycosaurs. The araeosceloids may be considered the counterpart, on the captorhinomorph side, of lizard-like procolophonids on the diadectomorph side of the Cotylosauria. *Araeoscelis* is best classified

within an infraorder, Araeoscelidia, coördinate with Limnosceloidea and Captorhinoidea under the suborder Captorhinomorpha, order Cotylosauria.

The araeosceloids, a lizard-like experiment of the early theropsid reptiles, seem to have left no descendants.

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EXPLANATION OF ABBREVIATIONS USED IN FIGURES

a, articular
ang, angular
bo, basioccipital
bt, basipterygoid process of the basisphenoid
c, coronoid
ca, anterior coronoid
d, dentary
e, exoccipital
ec, ectopterygoid
ep, epipterygoid
f, frontal
j, jugal
l, lacrimal
mx, maxilla
n, nasal
op, opisthotic
pal, palatine
par, parietal
pf, postfrontal
pmx, premaxilla
po, postorbital
pp, postparietal
pra, prearticular
prf, prefrontal
pro, proötic
ps, parasphenoid
pt, pterygoid
q, quadrate
qj, quadratojugal
s, stapes
sang, surangular
so, supraoccipital
sp, splenial
sq, squamosal
st, supratemporal
t, tabular
v, vomer

PLATE 1

Proximal portion of an immature humerus and an object possibly an independent bony epiphysis. The proximal end of the humerus, separated from the possible epiphysis by a band of matrix, faces the upper border of the picture; the preaxial edge of the humerus faces the left border. Note the transverse section of an immature vertebra near the upper border. UC 1708. x 10.

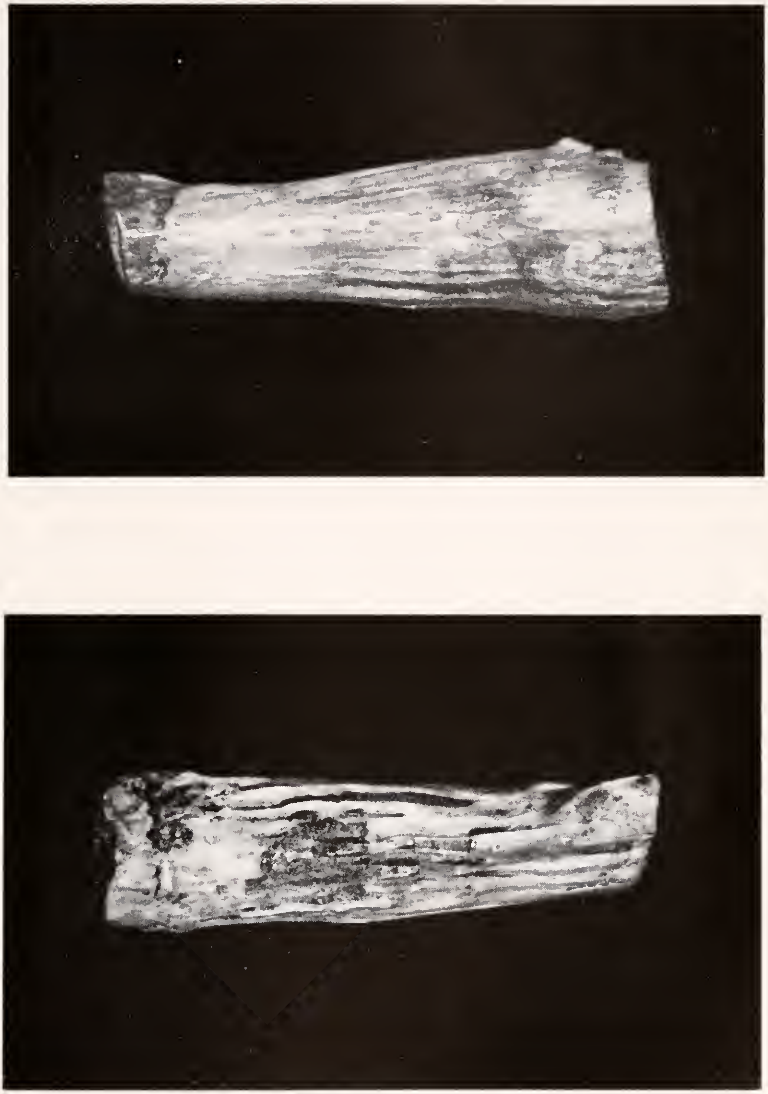

PLATE 2.

Two views of an object possibly a portion of a regenerated tail. MCZ 1262. x 4.

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

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A REVISION OF THE AUSTRALIAN ANT GENUS *NOTONCUS* EMERY, WITH NOTES ON THE OTHER GENERA OF MELOPHORINI

By William L. Brown, Jr.

CAMBRIDGE, MASS., U. S. A.

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No. 6—*A Revision of the Australian Ant Genus* Notoncus *Emery, with Notes on the other Genera of Melophorini*

By William L. Brown, Jr.

At the present time, *Notoncus* must still be listed among those formicine genera that are easy to recognize by habitus, but that cannot be adequately characterized in the formal sense. Fully limiting diagnosis will not be possible in these cases until the tribes and genera of the world Formicinae have been thoroughly examined and revised; the classifications of the subfamily and the tribes now in general use (Wheeler, 1922, 1935; Emery, 1925) are artificial and based on serious misconceptions. My colleagues, E. O. Wilson and T. Eisner, are now engaged in different phases of the work necessary to provide a skeleton revision of the tribes and genera of the Formicinae, but owing to the size and complexity of the task, final results will not be ready for several years.

The work already done by Wilson and Eisner, and a certain amount completed also by myself, has yielded a great deal of information on the phyletic distribution of important characters, such as proventricular structure and function, form and placement of propodeal spiracles, mandibular dentition in all castes, wing venation, male genitalia, and so on. While the work is not yet far enough advanced for us to predict what a natural tribal arrangement will look like, it will be sufficient to say that a new arrangement will differ considerably from those available. Insofar as the limits of tribe Melophorini are concerned, the same probably holds true, but for the purposes of this paper, we can continue to treat as melophorines the same genera listed in the most recent classification of the tribe (Wheeler, 1935). These genera have in common a "short" type of proventriculus (as contrasted with the "long" type of Formicini and Camponotini), and they are distributed in an "Antarctic" pattern more or less paralleling that of the unrelated ant groups *Heteroponera* Mayr and *Monomorium* (*Notomyrmex*) Emery. These characteristics do not, however, separate the Melophorini from other short-proventriculate groups that are well represented in the Southern Hemisphere (e.g., *Myrmelachista, Stigmacros*).

Wheeler's 1935 classification, while perhaps the best so far offered for the tribe, is so excessively synoptic that it is little more than a list of genera and subgenera, with type citations and a listing of the then included species. Wheeler avoided the diffi-

culty of characterizing the genera simply by omitting any reference to particular, concrete characters. The insight that afforded his classification a certain logic as compared to older systems was apparently a result of his second trip to Australia (1930-1931), and was derived at least in part from or in discussion with Clark (Clark, 1934). Neither Wheeler nor Clark ever attempted to place this system on a solid morphological basis. Here is Wheeler's 1935 generic arrangement of the Melophorini:

Myrmecorhynchus Emery
Lasiophanes Emery
Prolasius Emery
Pseudonotoncus Clark
Melophorus Lubbock
  subgenus *Melophorus s. str.*
  subgenus *Erimelophorus* Wheeler
  subgenus *Trichomelophorus* Wheeler
Notoncus Emery
Diodontolepis Wheeler

As already suggested, it is premature to consider that all of these groups really belong to a single tribe. If any genera were to be separated now, *Myrmecorhynchus* might be the most likely candidate for exclusion, as indeed it has been excluded in the past. Such questions are passed over here. *Myrmecorhynchus* is a genus inhabiting southeastern Australia, where it ranges from southeastern Queensland (Clark, 1934) to the western end of Kangaroo Island, South Australia (personal collection, unreported). It tends to be arboreal in foraging habits, and apparently some of the species normally nest in arboreal situations. With some patience, an investigator of these little-known ants should be able to trace individual workers to the nest by offering them honey baits. The specific identity of the genotype is uncertain, and may have been confused by Wheeler (1917). In 1934, Clark added descriptions of three species. I have found it impossible to determine specimens in my possession from the existing literature. This genus requires much closer study than it has had up to now.

Lasiophanes, the only neogaeic melophorine genus, is restricted to southern South America. The Argentinian species have been revised by Kusnezov (1951), who drastically reduced the number

of names by extensive synonymy. While this is not the final word on the species-level taxonomy of *Lasiophanes,* it is certainly a vast improvement over previous arrangements. *Lasiophanes* is supposed to differ constantly from other melophorines by the presence in the wings of the sexes of the medio-cubital crossvein (m-cu), which closes the discoidal cell, and by the confluence of the clypeal and antennal fossae. Present indications are that the genus contains not more than half a dozen closely related and rather variable species.

The Australian-New Zealand group *Prolasius* was raised by Clark and by Wheeler to generic rank distinct from *Melophorus,* an action that can now be supported by the discovery of good characters for separating these two genera (see below). Wheeler placed *Notoncus hickmani* Clark and *N. rotundiceps* Clark in the genus *Prolasius,* but it will be shown later in this paper that these really belong in *Notoncus.* The placement of *Melophorus scipio* Forel remains uncertain.

The species of *Prolasius* are medium-small to small in size, and black, brown, reddish or dull yellow in color. They resemble in habitus and to some extent in habits certain Holarctic species of *Lasius, Prenolepis* and some of the *Formica neogagates* group of North America, but they are generally more restricted ecologically than are their northern analogues, taken species for species. The nesting sites are restricted to those parts of Australia, including Tasmania, and New Zealand having a cool or temperate climate and good rainfall, and which therefore support a good forest cover. The workers show little or no polymorphism, their propodeal spiracles are small and round, and the mentum is without ammochaetae. Sculpture is reduced and fine, or smooth, and standing pilosity is usually sparse. Species taxonomy is reviewed in a paper by McAreavey (1947).

Pseudonotoncus Clark was based on the single species *Ps. hirsutus* Clark, from the Otway Peninsula of western Victoria. It is, however, widespread also in the vicinity of Melbourne, where I found it in medium-rainfall sclerophyll forest at Research and at Arthur's Seat above McCrae. The nests I saw were built in the soil without covering objects or detectable craters, and workers as well as frequent dealate females were found foraging over shrubs for nectar and honeydew. Donisthorpe (1937) described a color form, *Ps. turneri,* from Tamborine Mt., Queens-

land, but this is probably not specifically distinct from *hirsutus*. *Pseudonotoncus* is distinct from other melophorine genera in habitus and in possessing long, acute, paired propodeal and petiolar teeth.

MELOPHORUS Lubbock

Melophorus Lubbock, 1883, Jour. Linn. Soc. London, Zool., **17**: 51. Genotype: *Melophorus bagoti* Lubbock, 1883, monobasic.

< *Melophorus* (*Melophorus*), Emery, 1925, Genera Insect., **183**: 11 (see for further synonymy).

> *Melophorus* (*Melophorus*) Wheeler, 1935, Psyche, **42**: 71.

> *Melophorus* (*Erimelophorus*) Wheeler, 1935, *loc. cit.* Subgenotype: *Melophorus wheeleri* Forel, 1910, by original designation. New synonymy.

> *Melophorus* (*Trichomelophorus*) Wheeler, 1935, *loc. cit.* Subgenotype: *Melophorus hirsutus* Forel, 1902, by original designation. New synonymy.

After separating *Prolasius* and *Diodontolepis* from *Melophorus,* Wheeler divided the remaining Australian species into the three subgenera listed in the synonymy above. This division was said to have been made on the basis "mainly of thoracic structure," but Wheeler never revealed exactly what characters he had in mind. As already mentioned, concrete differential characters among the melophorine genera were ignored in Wheeler's 1935 classification; in their place, he substituted vague statements such as that *Melophorus* was "Cataglyphis-like," *Erimelophorus* "Pheidole-like," *Prolasius* "Lasius-like," and so forth. This looseness apparently misled McAreavey (1947), who found Wheeler's division of *Melophorus* "a useful one," and then proceeded to develop Wheeler's words "Pheidole-like" into "others harvest grain," but without citing the slightest bit of evidence for a habit which, in a formicine ant, would surely call for some documentation.

My own extensive observations on diverse *Melophorus* species referable to all three of Wheeler's subgenera, as found in desert, coastal dune and woodland habitats in many parts of Australia, do not include a single instance where any of the ants were found carrying seeds. On the contrary, all species were found to be fast-running predators of the *Myrmecocystus* and *Cataglyphis* class, so characteristic of arid Northern Hemisphere sections. As is well known, some of the species of *Melophorus* are "honey-

ants,'' with repletes analogous to those of *Myrmecocystus* spp. In my opinion, such lightning-quick predatory habits and honey- or nectar-feeding are complementary adaptations for xeric environments best developed in the Formicinae. In all of the same xeric localities in Australia (as well as in other parts of the world), one also finds myrmicine genera that are the true specialized harvesters; as a general rule these myrmicines forage, whether in search of seeds alone or of their usual mixed animal-vegetable diet, at a considerably more sedate pace.

The ''harvesting'' of seeds by formicines is not unknown, but the circumstances of such activities usually point to myrmecochoric adaptations of the seeds or to relationships other than the utilization of the entire seed contents as food by the ants. Myrmicines, on the other hand, can apparently draw nourishment from the entire contents of the seed that will sustain them over considerable periods of time. This is not true of many genera of myrmicines with predominantly insectivorous or otherwise specialized food habits, of course, and even the specialized harvesters among the myrmicines may require some animal protein for the survival of the nest economy. It should not be assumed that the presence of a polymorphic worker series including large-headed majors is evidence of harvester specialization like that of many *Pheidole* species, for such assumptions lead to obvious absurdities when the diversity of types of polymorphism among ants is considered (cf. Wilson, 1953). The seed-gathering activities of ants are treated by Bequaert (1922) and by Stäger (1929), both of whom cite further references.

My good friend Mr. John Mitchell, of the South Australian Museum, has called my attention to a note (Mitchell, 1948) on the environment of the agamid lizard *Tympanocryptis maculosa* Mitchell. This lizard was found on the salt-encrusted, four-mile-wide ''marginal area'' of the then long-dry Lake Eyre, in the desert of northern South Australia. Mitchell states that, ''In this barren habitat one immediately wonders as to the food of these lizards. An examination of the stomach contents has revealed it to consist mainly of small harvest ants (*Melophorus* sp.) which apparently feed on the numerous seeds which are blown out over the lake, or alternatively, as was suggested by Madigan (1930), on micro-organisms in the salt.'' On my query, however, I learned from Mitchell that the determination of the ants, and

their denomination as "harvest ants," were furnished by none other than Father McAreavey! It seems to me likely that Madigan's opinion has the better chance of being correct, and I may mention also that I have observed on other dry Australian salt lake-beds that not only seeds, but also winged insects in large numbers, are blown far out onto the uninhabitable crust. In addition, a few kinds of insects appear to be at home on the salt crust.

No matter what harvesting propensities or lack of them among *Melophorus* species may eventually be demonstrated, I still fail to find any fundamental differences between the species Wheeler assigns to *Melophorus s. str.* and those he puts in *Erimelophorus*. Both "groups" produce large-headed soldier forms, and interspecific variation in alitruncal structure runs without any particular regard for his suggested division. The subgenus *Trichomelophorus* is based on an admittedly aberrant species, *M. hirsutus* Forel, but even here the alitrunk is not so markedly different in basic structure as to suggest a split on this character alone. The subgeneric name suggests that Wheeler was unduly impressed by the striking long and abundant pilosity, but if so, then he did not take into proper account the fact that another undetermined *Melophorus* in his own collection combines very similar pilosity with a more nearly "typical" *Melophorus* alitrunk. In short, I am unable to support Wheeler's subgenera on either morphological or ethological grounds.

On the other hand, I have now seen a majority of the Australian Melophorini species, and I am impressed by a set of characters that will, I believe for the first time, permit objective diagnosis of *Melophorus* (*s. lat.*) as a distinct genus. The following remarks refer only to the worker and female castes. Most *Melophorus* have elaborate and well-developed sets of ammochaetae on the gula, mentum, clypeus and mandibles. In a few small forms inhabiting more mesic areas, the ammochaetae may be much reduced. Nevertheless, if the extensive and varied sample I have seen is fully representative, the ammochaetae are never wholly lost in any true *Melophorus*. In all species I have seen, at least one or two pairs of sturdy, long, J-shaped hairs are to be found arising from the base of the mentum, their tips curving anteriorly under the mandibles. In exceedingly hairy forms, such as *M. hirsutus,* the mental ammochaetae may be difficult to see, and in

worn or damaged specimens they may occasionally be missing, but the coarse pits from which they arise can always be found under high enough magnification or by dissection.

Another character is easier to use, and this has been found perfectly correlated with the ammochaetal character in all species reviewed. This concerns the shape of the propodeal spiracles, which in *Melophorus* are narrow and elongate, in the form of a slit or comma.

In melophorines of all other genera, in all of the many species I have examined, ammochaetae are absent from the mentum, and the propodeal spiracles are round or broadly oval. *Melophorus* is usually rather highly polymorphic in the worker caste, but this character is difficult to utilize for practical identification, and it is not an absolute generic difference among the melophorines. Two possibly aberrant species I have never seen, and which are incompletely described: *M. fulvihirtus* Clark and *M. scipio* Forel, are placed in *Melophorus* with doubt.

In Australia, to which country *Melophorus* is apparently confined, the genus is commonest in arid regions, especially in the central and southern parts, and several species occur on both littoral and inland dune systems. A few small species occur in medium-rainfall forest types, but the wettest forest types appear to exclude them in favor of *Prolasius* and other genera. In general, *Melophorus* is impoverished in mesic environments, and the ammochaetae and narrowed propodeal spiracles, obvious adaptations to a xeric habitat, make it likely that the genus arose in response to the increasing availability of arid situations back in the geologic past of the continent. The ancestral stock may have been *Prolasius*.

Notoncus Emery

Notoncus Emery, 1895, Ann. Soc. Ent. Belg., **39**: 352. Genotype: *Camponotus ectatommoides* Forel, 1892, monobasic.

> *Notoncus* Emery, 1925, Genera Insect., **183**: 14. Wheeler, 1935, Psyche, **42**: 71.

> *Diodontolepis* Wheeler, 1920, Psyche, **27**: 53. Genotype: *Melophorus spinisquamis* André, 1896, by original designation, monobasic. Clark, 1934, Mem. Nat. Mus. Victoria, Melbourne, **8**: 64. Wheeler, 1935, Psyche, **42**: 70. New synonymy.

< *Melophorus* (*Melophorus*), Emery, 1925, Genera Insect., **183**: 12.

Had we to deal here only with the species placed in *Notoncus* before 1930 (*ectatommoides, gilberti* and *enormis* in the sense of this paper), generic diagnosis would be simplicity itself, for the workers of these species all have the pronotal humeri and scutellum hypertrophied and unusually salient in one form or another. Unfortunately for this neat little arrangement, Clark described in 1930 two species, *N. hickmani* and *N. rotundiceps,* that are very like the "typical" *Notoncus,* but in which the hypertrophy of the alitruncal components is suppressed and ambiguous. Actually, Clark's two species appear to be large and small allometric variants of one species, *N. hickmani* (*q. v. infra*), but this does not affect the status of this species with respect to generic placement.

Wheeler (1935) shifted Clark's species into *Prolasius,* but McAreavey rejected this placement because he was misled by the original descriptions into thinking that the types, unlike *Prolasius* workers, were without ocelli. However, ocelli can be demonstrated in *hickmani* workers, particularly the larger ones, under good circumstances. The presence of ocelli does not make *hickmani* a *Prolasius,* for there exist differences of habitus that I believe most myrmecologists will accept until the proper study of *Prolasius* enables us to state satisfactory generic characters for that group. The current taxonomy of *Prolasius* (Clark, 1934; McAreavey, 1947) does not seem to me to reflect very accurately the species in collections I have seen.

The really significant relationships of *N. hickmani* appear to me to be with the three "typical" *Notoncus* species on one side, and with *Diodontolepis spinisquamis* (André) on the other; in fact, I regard *hickmani* as the perfect intermediate linking these superficially disparate types in one genus. The alternative to this merger would be the segregation of *hickmani* and *spinisquamis* in one genus (*Diodontolepis*) apart from the "typical" *Notoncus,* but in this case, the generic split would have to rest entirely, so far as known characters go, on the degree of hypertrophy of the elements of the alitrunk already mentioned. The larger workers of *hickmani* clearly show a tendency toward hypertrophy, however, and certain series of *N. enormis* (and perhaps other species) show such general damping of the usual hypertrophied elements that the specialist becomes aware that any dividing line drawn on this basis is ambiguous with respect

to at least some nest series. The development of the various elements of the alitrunk appears to respond in a correlated way to an overall genetical factor controlling the general degree of hypertrophy, and it is the instability and gradational nature of this factor that prevents us from using it as a generic character. Other points of similarity, at least in the female and worker castes examined, indicate close relationship of *spinisquamis* and *hickmani* to the other *Notoncus*, and their separation on the present evidence would be arbitrary and of little practical taxonomic value. Emery (1925) had retained *spinisquamis* in *Melophorus*, but in this he was mistaken (Clark, 1934; Wheeler, 1935). It can now be shown that all of the species here included in *Notoncus* lack the mental ammochaetae of *Melophorus* and possess round or nearly round propodeal spiracles.

The species of *Notoncus* are medium-small to medium in size, with color ranging from yellow to piceous. Internidal allometry is often marked, and *enormis* shows sufficient intranidal allometry over its usual size range that it deserves to be called "polymorphic"; however, even *enormis* cannot rival in this respect the more highly polymorphic species of *Melophorus*.

The species of *Notoncus* are, so far as known, confined to Australia, including Tasmania. All five of the species are found in eastern Australia, and two of them occur sporadically through the less extremely arid parts of South Australia, to reappear in southwestern Australia. The distributions of the species are summarized in greater detail below.

A Summary of Species-Level Taxonomy in *Notoncus*

Unfortunately for later developments in species-level taxonomy of the genus, the workers Emery described and figured in 1895 as "*ectatommoides*" are not the corresponding caste of the original female type of Forel's *ectatommoides*. The females and workers of all the valid *Notoncus* species have now been properly associated, and it is reasonably clear from Forel's original *ectatommoides* description that he had a specimen agreeing with the characters as given for that species in the key to the females below. Emery's workers belong to the species described by Szabó as *enormis*, which is the first available name, and the one adopted here. The worker and female of *enormis* match in having the gastric dorsum densely pubescent, and they differ from the

respective castes of *ectatommoides* by the same character.

The species *capitatus* Forel and *capitatus* var. *minor* Viehmeyer are obvious synonyms of *enormis* described through a lack of appreciation of the polymorphism shown by this species. *N. mjöbergi* refers to the variant, sporadic in Queensland, in which the hypertrophy of the humeri and scutellum is relatively more or less feebly expressed; intergradient forms prevent our accepting it as a distinct species, and there is no clear evidence that it forms geographically distinct populations in eastern Queensland.

The species *ectatommoides*, previously resting on a single female labelled "New Zealand," was recognized by both Forel and Emery as an Australian endemic. The accompanying species with similarly erroneous locality labels were indicative of a South Australian provenience, and it is quite possible that *ectatommoides* was first taken in the vicinity of Adelaide. Donisthorpe's species *rodwayi*, also described from a female, does not seem to differ in any significant way from the *ectatommoides* type, and I feel confident that it is a synonym on the basis of descriptions and considerations of locality. The worker associated with the *ectatommoides* female (in the same nest series) agrees well with the description of *foreli* by André or with the descriptions of one of the *foreli* varieties described later. André cited the original locality of *foreli* as "Australie occidentale," but this may be in error. This species has not been reported since from Western Australia, despite considerable myrmecological exploration of that state; on the other hand, in the same paper wherein André described *foreli*, he described several other ant species from the "Alpes de Victoria." The *Notoncus* species in question is very common in the Victorian Alps, and there is little question from all the descriptions concerned that *foreli* and the varieties *dentata*, *subdentata* and *acuminata* are all representative of the highly variable species properly called *ectatommoides*.

N. gilberti Forel is a smooth form related to *enormis;* it has several named subspecies and varieties, all synonymized under the species heading below, and *politus* Viehmeyer seems from the description to be an obvious synonym.[1]

[1] The Australian ant species of Viehmeyer were mostly published posthumously, apparently in large part from incomplete notes. It is by no means certain that Viehmeyer himself would have gone through with the publication of all these forms as novelties had he lived long enough, for a large proportion in all subfamilies belongs in the obvious synonymy of well-known species. Such posthumous publications, arranged by well-meaning friends of the deceased as his last memorial, are more likely to end by ruining his reputation. The section of posthumous papers in the "Cho Teranishi Memorial Volume," published in Japan by Teranishi's friends in 1940, is a similarly unfortunate case.

N. hickmani (=*rotundiceps*) and *N. spinisquamis* are relatively uncomplicated cases taxonomically, completing the roster of the genus as known at present. A synoptic list of the species and synonyms is offered below as a clarifying summary of changes here proposed in the species-level taxonomy of *Notoncus*.

N. ectatommoides (Forel), 1892
  =foreli André, 1896, n. syn.
  = " var. dentata Forel, 1910, n. syn.
  = " var. subdentata Forel, 1910, n. syn.
  = " var. acuminata Viehmeyer, 1925, n. syn.
  =rodwayi Donisthorpe, 1941, n. syn.
N. enormis Szabó, 1910
  =ectatommoides *sensu* Emery, 1895, *nec* Forel.
  =capitatus Forel, 1915, n. syn.
  =mjöbergi Forel, 1915, n. syn.
  =capitatus var. minor Viehmeyer, 1925, n. syn.
N. gilberti Forel, 1895.
  = " var. gracilior Forel, 1907, n. syn.
  =politus Viehmeyer, 1925, n. syn.
  =gilberti annectens Wheeler, 1934, n. syn.
  = " " var. manni Wheeler, 1934, n. syn.
N. hickmani Clark, 1930.
  =rotundiceps Clark, 1930, n. syn.
N. spinisquamis (André), 1896, n. comb.

A Summary of the Known Distribution of the Five Species

The full ranges of each of the species differ, but there is broad overlap. In any one circumscribed and ecologically uniform area, there are no known cases where more than two of the species occur together. The most abundant and successful species within its range, and also the most variable structurally, is *ectatommoides,* which is abundant in the more open, grassy areas from east-central Queensland south through southeastern Australia to the Flinders Ranges and the vicinity of Adelaide. The extremes of environment occupied are the cool, moist mountain forest of grassy-floored intermediate sclerophyll type, common in the Australian Alps, and the arid, semi-oasic pockets in and near the Flinders Ranges, such as that at Wilpena Pound. Trees of moderate to large size seem always to be within foraging dis-

tance of the nests. In mallee, open woodland and heath country in Victoria and South Australia, *hickmani* tends to replace *ectatommoides* in many areas.

In Western Australia, on the far side of the barren Nullarbor Plain and its flanking arid tracts, *hickmani* is found again in the Perth-Albany "corner," a section in which, as already discussed above, the true *ectatommoides* probably does not occur. The only other *Notoncus* species certainly known from southwestern Australia is *gilberti* Forel, which appears to be abundant in the Perth district, and which is closely sympatric with *hickmani* in at least some areas east to Norseman and Esperance.

N. gilberti is not found again until, coming eastward, one meets with a restricted colony in the Flinders Ranges of South Australia; in one locality here, *gilberti* was found nesting very obscurely in the most heavily shaded and moist habitat available, in an area very densely populated by *ectatommoides*. After the Flinders Ranges oases, *N. gilberti* is found sporadically through eastern New South Wales and Queensland, in most cases, apparently, within the range of *ectatommoides*, and often at the same exact localities as the latter. The head form of worker and female *gilberti* resemble those of certain parasitic ants, and it is not beyond possibility that *gilberti* founds its nests by parasitizing species like *ectatommoides* (in the eastern states) and *hickmani* (in southwestern Australia). It should be emphasized that such a relationship is at present purely speculative.

N. spinisquamis and *N. enormis* live in or on the margins of very wet forests in eastern Australia; *spinisquamis* appears to occupy the cooler wet sclerophyll forests of Victoria and Tasmania, while *enormis* exists in the more tropical forests of eastern New South Wales and Queensland, farther to the north; both species exclude from their domains the widespread *ectatommoides*, which accompanies them through most of their ranges in adjacent intermediate vegetation types, but does not enter the wettest forest when they occur there.

At present, our knowledge of the distribution of all of these species and of their ecological limitations, diurnation of foraging, etc., is only very fragmentary. For this reason, we cannot say with confidence whether the seeming geographical variation in "habitat preference" is correlated with the distributions of various potential competitors; but in stating my preliminary

hunch, I believe that this will be found to be the case when *Notoncus* is better known. From a combination of morphological and distributional evidence, we may be safer in designating *spinisquamis* and *hickmani* as primitive types within the genus; it seems likely that *gilberti*, *enormis* and *ectatommoides* arose from something like *hickmani*.

Our knowledge of the habits of *Notoncus* species is very limited. The general method of nest-founding is probably of the claustral type, usual among formicines (see account of nuptial flights below), with reliance on a single dealate female. The nests are made in the soil, usually without covering rocks or other objects; the galleries extend beneath rocks more frequently in mountainous localities with high rainfall. The nests are most often, perhaps always, built near trees or large shrubs; in the few cases in which I have observed them directly, the *Notoncus* appeared to be climbing the trees for sugar secreted by various homopterans, but these cases were not favorable for the direct determination of the methods used by the ants in securing the honeydew. On a few occasions, root coccids or aphids have been observed in groups in the galleries of *N. ectatommoides.* Foraging activities take place outside the nest and above-ground, and all the species appear to be nocturnal or crepuscular foragers in varying degrees; diurnation of foraging activities, however, is highly variable with the seasons and with differing habitats, and possibly also according to the potential competitors present.

The nests are rather populous, in my experience, though this may not be obvious from superficial excavations made during the daytime, when most of the ants are at lower levels in the nest. The nests may extend over considerable territory without showing noticeable outward signs of their presence except, perhaps, for very small, irregular piles of excavated soil scattered at intervals in such a way as to be nearly imperceptible to the casual searcher. The workers run fairly rapidly, and tend, especially during the daytime, to take advantage of whatever cover exists in the form of soil-surface litter or loose bark on tree trunks. When the nest is breached, the workers show little aggressiveness, and hide readily whenever possible; however, they do show persistence and efficiency in removing the brood to safety.

Records for the production and nuptial flight of the winged sexes show wide seasonal variation within and between species;

our data are still too scanty to show a general pattern. Probably the flight time is controlled by temperature-humidity factors that reach optima at different times in different parts of the continent.

G. C. and J. Wheeler (1953, pp. 130, 211, pl. 1, figs. 6-11) have described the larva of *N. ectatommoides* (=*N. foreli*) in their comparative study of formicine larvae. Possibly in part as a result of ideas I once expressed to them in a letter, the Wheelers speculatively suggest the possibility that the ectatommine ponerines may have given rise to the original *Notoncus* stock. I have since had the opportunity to study the adult morphology of both *Notoncus* and the Ectatommini in much greater detail, and in relation to a fairly satisfactory general scheme of ant phylogeny (Brown, 1954), with the result that I must now consider *Notoncus* and the ectatommines to have come from very different basic formicid stocks. Under this interpretation, such suggestive similarities as exist must be considered as due to convergence.

Key to the species of NOTONCUS: *workers*

1. Scutellum hypertrophied, projecting dorsad as a rounded tumulus or ovoid process, or as an erect scale, furcula, or tooth, from the region between the mesonotum and propodeum; humeri strongly developed, angulate and salient .... 2.
   Scutellum absent, or at best not sharply differentiated and not forming any kind of prominent process projecting dorsad (in some workers of *N. hickmani*, the metanotal spiracles may be connected by a cariniform vestige); humeri rounded, not projecting to any marked extent .... 4.
2. Scutellum in the form of a slender, erect process, the apex of which may be in the form of a chisel point, an emarginate chisel point, a Y, a thick, pointed tooth, or some intermediate shape (s. Queensland to S. Australia, sporadic in dry inland areas) .... *ectatommoides* (Forel)
   Scutellum in the form of a thick, rounded tumulus or ovoid process 3.
3. Alitrunk at most very finely and superficially sculptured, so that it can be described as smooth and shining; gastric dorsum with only extremely sparse punctulation and appressed pubescence; mandibles finely striate over most of dorsal surfaces. (N. S. Wales, e. Queensland, sw. Australia, sporadic in Flinders Ranges of S. Australia) .... *gilberti* Forel
   Alitrunk distinctly, widely, and rather coarsely striate, and largely subopaque throughout; gastric dorsum densely punctulate and with dense appressed pubescence; mandibles largely smooth and shining above, with coarse punctures (moist subtropical and tropical forests of e. Queensland and N. S. Wales) .... *enormis* Szabó

4. Large, slender species with long appendages, the antennal scapes much longer than (usually at least 1.2x) the length of the head proper, including clypeus (Victoria, Tasmania) .... *spinisquamis* (André)
   Smaller, more robust species, the antennal scapes rarely, if ever, longer than the head proper, including clypeus, and usually shorter (widespread in se., South and sw. Australia) ....*hickmani* Clark

Key to the species of NOTONCUS: *females*

1. Antennal scapes much longer than head proper, including clypeus (ratio usually about 1.2: 1.0); large, usually yellowish form with long legs... .... *spinisquamis* (André)
   Antennal scapes usually shorter than, rarely about equal to, length of head proper, with clypeus .... 2.
2. Normally exposed surfaces of gastric dorsum densely micropunctulate and with dense appressed pubescence .... *enormis* Szabó
   Gastric dorsum with at most very sparse and inconspicuous punctulation and pubescence .... 3.
3. Dorsal surfaces of mandibles largely smooth and shining, with scattered coarse punctures; striation absent or limited to feeble peripheral remnants .... *ectatommoides* (Forel)
   Dorsal surfaces of mandibles finely striate over all or nearly all of their dorsal surfaces, in addition to the coarse punctation usually present here .... 4.
4. Head in dorsal full-face view subrectangular, with nearly straight sides, rather abruptly rounded occipital angles, and transverse, feebly convex posterior border .... *gilberti* Forel
   Head in dorsal full-face view ovoid, with strongly convex sides and broadly rounded occipital angles .... *hickmani* Clark

SYSTEMATIC TREATMENT BY INDIVIDUAL SPECIES

NOTONCUS ECTATOMMOIDES (Forel)

Camponotus ectatommoides Forel, 1892, Mitt. Schweiz. ent. Ges., **8**: 333, female. Type locality: probably [South] Australia, though original label of genotype indicated New Zealand as locality. Holotype: apparently in Mus. Civ. Stor. Nat., Genova, Italy.

Notoncus ectatommoides, Emery, 1895, Ann. Soc. Ent. Belg., **39**: 353, female, *nec* worker.

Notoncus foreli André, 1896, Rev. Ent., Caen, p. 256, worker. Type locality: ''Australie occidentale,'' probably in error; see above in the summary of species-level taxonomy in *Notoncus.* The type probably came from the Australian Alps. Holotype: Mus. Hist. Nat., Paris. New synonymy.

Notoncus foreli var. *dentata* Forel, 1910, Rev. Suisse Zool., **18**: 68, worker. Type locality: Gembrook, Victoria. Syntypes: Mus. Hist. Nat., Geneva. New synonymy.

Notoncus foreli var. *subdentata* Forel, 1910, *ibid.*, p. 68, worker. Type locality: Forset Reefs, New South Wales. Syntypes: Mus. Hist. Nat., Geneva. New synonymy.

Notoncus foreli var. *acuminata* Viehmeyer, 1925, Ent. Mitt., **14**: 37, worker. Type locality: none cited; by inference eastern New South Wales. Syntypes: probably in Anthrop. Zool. Mus. Dresden. New synonymy.

Notoncus rodwayi Donisthorpe, 1941, Ann. Mag. Nat. Hist. (11), **8**: 206, female. Type locality: Nowra, New South Wales. Holotype: Brit. Mus. (Nat. Hist.). New Synonymy.

The worker of this species is variable in size, color, sculpture, angularity of propodeum, etc., and shows a wide range in the form of the upwardly projecting scutellum (see key to workers). However, the scutellum never approaches the tumuliform or ovoid shapes seen in the scutellar outgrowths of the related *N. gilberti* and *N. enormis*. The alitrunk and head are usually extensively and irregularly striate in varying directions, and the color ranges from light red-brown to piceous. Variation in most of the obvious characters appears to be partly size-linked (allometric), and partly independent of size. The largest and darkest forms seen, speaking in terms of averages, are those from the dry inland areas such as Wilpena Pound and Mildura. These more or less isolated (oasic) populations also show strong sculpture and tend to have the most strongly bifurcate or bicornuate scutellar apices. Series from the wet Dandenong Ranges, near Melbourne, are also dark, and are only slightly less heavily sculptured, but there is extensive local and intranidal variation in sculpture and in the depth of emargination of the scutellar apex. Populations from the dry, warm savannah woodland of southeastern Queensland tend to be smaller, smoother, lighter in color, and more often have the scutellum reduced to a chisel-pointed, or even a slender, acutely pointed process, though here again individual variation is very great. Population samples from intermediate areas and from the environs of Adelaide show all combinations of intergradient conditions connecting the forms described, and, except for the size-linked tendencies, geographical variation of independent characters seems to be highly discordant. Most of the various character-combinations seem to be very local, and all clinal trends are expressed crudely, at best.

The synonymy of this species has already been discussed in the summary of species-level taxonomy within the genus (above). An intensive study of the geographical variation in this species should prove to be most interesting; in many places it is a dominant ant, while in other places appearing suitable to the human eye, it is totally absent. The samples available may represent each a well-marked deme, but collecting has not yet been extensive enough to indicate the amount of discontinuity affecting the range of the species.

Localities for material studied: QUEENSLAND: Bundaberg (A. M. Lea). Brisbane (H. Hacker; B. Blumberg). Enoggera (W. M. Wheeler). Montville and ridge above Obi-obi River, Blackall Range, 300-500 m., pasture and lawn cleared from rain-forest (W. L. Brown). Moggill, savannah woodland (Brown). NEW SOUTH WALES: Uralla; Salisbury Court (Wheeler). Albury (F. E. Wilson). Coff's Harbour, dry sclerophyll forest (Brown). VICTORIA: Ferntree Gully (F. P. Spry; Brown). Mt. Dandenong, 2000 feet, and One Tree Hill, Dandenong Ranges, grassy-floored moist sclerophyll forest, abundant (Wheeler; Brown). Vermont; Burwood, intermediate lowland sclerophyll forest (Brown). Mildura (F. H. Taylor). SOUTH AUSTRALIA: "Adelaide" (W. Pennifold). Wilpena Pound, Northern Flinders Ranges, dry *Callitris*-red gum savannah woodland, abundant (Brown).

Nuptial Flight

A nuptial flight of this species was witnessed along the summit ridge of the Blackall Range, in and near Montville, Queensland, on May 21, 1951, beginning at about 11 A.M. on a fine, warm, sunny day. Earlier on the same morning heavy rains lasting through the previous week had ended, leaving the ground thoroughly saturated. In a cropped lawn at Montville, numerous small holes appeared, each opened by workers and accompanied by a minute pile of dark earthen particles. From these holes, males began to issue almost immediately in numbers, until within a few minutes there had accumulated on the surface a surprisingly large number of this sex and also a few workers. The males travelled aimlessly over the sward in low, flitting flight from one blade of grass to another, never rising more than a foot or so from the ground. Movement seemed to take place at random in

all directions. Suddenly, however, the males of one area all rushed simultaneously to a single focal point, which proved to be a winged female emerging from a small hole. In a few seconds, the female was surrounded by a dense swarm of males in the form of a ball, which at times must have exceeded 2 cm. in diameter. This ball moved in a half-tumbling, half-dragging motion over and among the densely packed grass blades, and held together for perhaps 20 seconds, after which the female escaped, flying straight upward. She appeared not to be encumbered by a male, and no males were seen to follow her for more than a foot above the ground; she flew steadily, and soon passed out of sight.

Meanwhile, the lawn had become dotted with similar balls of frenzied males, each surrounding a female in a fashion similar to the first. Obviously, many more males than females were involved in this particular flight. On each occasion, the female left the ball after 20-30 seconds and flew straight upward. I was not able to see whether all were unaccompanied by males, but none of those I saw up close had consorts in its flight after the first foot or so of the ascent. It is impossible to say, from these observations, whether mating takes place in the ball-formation on the ground, but this is my general impression, based on the lack of inclination in the observed males to fly at any distance above the ground.

During about 10 minutes, after which time the flight had begun to decline from peak activity, the males continued to search low over the grass, participating in each ball-formation encountered. About a half hour after the first appearance of the females, only males were to be seen flitting here and there or resting on grass blades. A few were seen visiting low flowering shrubs on a nearby fence row. At that time, I had to leave the scene, and the flight appeared to be at an end, with no more females appearing and the males rapidly disappearing by what appeared to be simple horizontal dispersal. No descending or dealate females were seen at this site at this time or later.

At 1 P.M. on the same day, on a part of the ridge about two airline miles distant, stray winged females of this species landed on my clothing while I was walking along a trail in sloping pasture. Others were found dealate, running over grass and bare spaces. No males were seen. At this place, a single dealate female of *N. enormis,* also apparently fresh from nuptial flight, was

found running over the open turf with the *ectatommoides,* though no nests of *enormis* were found by me in the Blackall Range.

The flight of *ectatommoides* was clearly an extensive and coordinated one over all or most of the ridge on that particular day, and was remarkable for the numbers of individuals produced. Previous collecting had indicated a rather modest population of the species, mostly nesting under stones, but the emerging males and females outlined instead, at least in one limited area within my range of view, a virtual continuum of underground galleries throughout lawn and pasture. A similar phenomenon occurs in the case of the flights of *Acanthomyops* species in North America and *Acropyga* in the Orient, both of which groups are subterranean in habits, and hence seldom suspected to be present in any numbers outside the flight season.

Notoncus enormis Szabó

Notoncus ectatommoides Emery, 1895, Ann. Soc. Ent. Belg., **39**: 353, fig. 4, worker, *nec* female, *nec* Forel. Kamerunga, Queensland.

Notoncus enormis Szabó, 1910, Ann. Mus. Nat. Hungar., **8**: 368, fig. 6, worker. Type locality: Mt. Victoria, New South Wales. Holotype: Hungarian National Museum, Budapest.

Notoncus capitatus Forel, 1915, Ark. f. Zool., **9** (16): 90, pl. 1, fig. 8, worker. Type locality: Tamborine Mt., Queensland. New synonymy.

Notoncus mjöbergi Forel, 1915, *ibid.*, p. 91, worker. Type locality: Colosseum, Queensland. The types of this and the preceding species are probably in the Naturhistoriska Riksmuseet, Stockholm, and in the Forel Collection in the Geneva Museum. New synonymy.

Notoncus capitatus var. *minor* Viehmeyer, 1925, Ent. Mitt., **14**: 139, worker. Type locality: none cited; by inference, eastern New South Wales. New synonymy.

N. enormis is the most polymorphic among the *Notoncus* species as presently known. In the largest workers, the head is proportionately broader than in the smaller ones, and is more reddish in tone. The female is large and bulky, larger than in any of the other forms except the very large *spinisquamis*. Both worker and female are readily distinguished by the opaque sculpture and particularly by the well developed reclinate pubescence of the body in general, including the gastric dorsum. The worker scutellum, like that of *gilberti,* is rounded and projecting, but it varies more in size from series to series. A series from Bribie

Island, Queensland, follows Forel's description of *mjöbergi* in having a small, low scutellum, but this appears to be nothing more than an extreme in the normal variation of *enormis*. The synonymy has been discussed briefly under the heading of species-level taxonomy in the genus (above).

N. enormis is locally abundant in rainforest and subtropical wet sclerophyll forests, or their borders, clearings or successional stages, through eastern New South Wales and Queensland, north at least as far as the Cairns district of northern Queensland.

Localities for material studied: QUEENSLAND: Tamborine Mt., rainforest, second-growth forest of *Eucalyptus gigas,* and bordering cleared pasture land (A. M. Lea; W. L. Brown). Near Kondalilla Falls, Blackall Range, female just after nuptial flight, May 21, 1951 (Brown). Kuranda (Brown). Bribie Island (H. Hacker). NEW SOUTH WALES: Moree (A. M. Lea). "Near Sydney" (without collector). Katoomba (W. M. Wheeler). Bulli (F. H. Taylor). Dorrigo (W. Heron).

NOTONCUS GILBERTI Forel

Notoncus Gilberti Forel, 1895, Ann. Soc. Ent. Belg., **39:** 418, worker, female. Type locality: Mackay, Queensland. Syntypes: Mus. Hist. Nat., Geneva.

Notoncus Gilberti var. *gracilior* Forel, 1907, in Michaelsen and Hartmeyer, Fauna Südwest-Austral., Jena, **1:** 299, female. Type locality: Fremantle, Western Australia. Holotype: Mus. Hist. Nat., Geneva? New synonymy.

Notoncus politus Viehmeyer, 1925, Ent. Mitt., **14:** 39, worker. Type locality: Liverpool, New South Wales. Syntypes: Anthrop. Zool. Mus. Dresden? New synonymy.

Notoncus gilberti subsp. *gracilior* Wheeler, 1934, Jour. Roy. Soc. W. Australia, **20:** 153, worker, female.

Notoncus gilberti subsp. *annectens* Wheeler, 1934, *ibid.*, p. 154, worker. Type locality: Enoggera, Queensland (by present selection); additional original locality, Brisbane, Queensland. Syntypes: Mus. Comp. Zool., Harvard. New synonymy.

Notoncus gilberti annectens var. *manni* Wheeler, 1934, *idem,* p. 155, worker. Type locality: Como, near Sydney, New South Wales (by present selection); additional original locality, Hornsby, New South Wales. New synonymy.

The worker of this species is very similar in the form of the alitrunk to *N. enormis,* but the sculpture is reduced to at most a very fine, loose, superficial reticulation, so that to all intents the

integument can be called smooth and shining, or even "polished." The mandibles, however, are finely striate over the usual scattered punctures, and the striation covers nearly the whole of their exposed dorsal surfaces; the clypeus is more or less distinctly longitudinally striate. The head in both castes, especially the female, is distinctly rectangular in full-face outline, with nearly straight sides, sharply rounded occipital corners, and a transverse, only feebly convex posterior occipital border.

Wheeler's 1934 subdivision of *gilberti* calls attention to the geographical variation, involving an apparent east-west size difference, plus other distinctions of size, color, sculpture, etc. supposed to mark different populations. However, the differences cited by Wheeler seem to be somewhat overdrawn; the smaller size of the western population is an average, not an absolute difference, and the samples from both east and west are still far from sufficiently representative for the purpose of testing significance of such variation. Even Wheeler recognized that some of the eastern samples were intergradient (subsp. *annectens!*), and then he never took into account Viehmeyer's obvious synonym, *N. politus*.

New material includes the piceous-colored examples from the hills around Canberra, and the isolated population sample from the Northern Flinders Ranges. These series add new dimensions to problems of geographical variation in the species, and at the same time show how inadequate our previous information was, and probably still is. For the time being, I prefer to emphasize the obvious kinship of all of the known samples by including them in the single species *gilberti*, without further distinction. Any future subdivision will have to take into account the realities of reproductive isolation between the various populations before it is formally made.

Localities for material studied: QUEENSLAND AND NEW SOUTH WALES: Type series of forms described by Wheeler; see synonymy, above. AUSTRALIAN CAPITAL TERRITORY: Kowen Forest, under rocks in open upland sclerophyll woodland, dark piceous variant (T. Greaves and W. L. Brown). SOUTH AUSTRALIA: Wilpena Pound, N. Flinders Ranges, under stone in entrance gorge, heavy riparian woodland of large *Eucalyptus camaldulensis* (Brown). WESTERN AUSTRALIA: Rottnest I.; Geraldton; Cottlesloe; Monger's Lake, near Perth

(W. M. Wheeler). King's Park, Perth (Wheeler; P. J. Darlington). Esperance; Norseman (E. O. Wilson). Wheeler took winged and newly dealate females near Perth on October 17 and 19, 1931.

Notoncus hickmani Clark

Notoncus hickmani Clark, 1930, Proc. Roy. Soc. Victoria (n.s.) **42**: 126, fig. 1, no. 14, worker, female. Type locality: Trevallyn, Tasmania. Syntypes: Nat. Mus. Victoria, Melbourne.

Notoncus rotundiceps Clark, 1930, Proc. Roy. Soc. Victoria (n.s.) **42**: 127, fig. 1, no. 15, worker. Type locality: Albany, Western Australia. Syntypes: Nat. Mus. Victoria, Melbourne. New synonymy.

This species is smaller, more hairy (especially the underside of the head), and has proportionately shorter appendages than *N. spinisquamis,* and the gaster is oftener dark in color — in many series it is piceous. Size is very variable, both within and between nests of this species, and there exist partly allometric differences in head shape, alitruncal form, distinctness of ocelli, and completeness of striate sculpture; these differences appear to have been Clark's basis for separating the species *rotundiceps* from the original *hickmani.* Series at present available seem to indicate that Victorian-Tasmanian series from the higher-rainfall districts are larger on the average than those from New South Wales, the Victorian Mallee, South Australia and southwestern Australia; round-headedness and effacement of sculpture is in general correlated directly with the smaller size classes, but coloration is poorly correlated geographically with these qualities. Series from drier localities often seem lighter in color, regardless of size and sculpture.

N. hickmani occupies drier sites than does *N. spinisquamis;* in the Melbourne district, I found *hickmani* in open sclerophyll forest to the east of the city, and on the savannah to the north, in both places nesting at the bases of eucalypt trees. On the savannah at Broadmeadows, ants of this species were found on a cool, wet winter day resting in small groups beneath chips and bark lying on the ground at some distance from the nest. The ants forage at night on trees and shrubs.

Localities for material studied: In addition to syntypes of *hickmani* and *rotundiceps,* series from the following — NEW

SOUTH WALES: Dorrigo (W. Heron). VICTORIA: Sea Lake (J. C. Goudie). Burwood; Broadmeadows (W. L. Brown). SOUTH AUSTRALIA: Adelaide, dealate female in spider web, 16/V/04 (A. Zietz). Mt. Lofty (J. O. Tepper). Lucindale (Feuerheerdt). Encounter Bay (collector?). Sandy Creek (J. O. Tepper) and Ravine des Casoars (Brown), both on Kangaroo I. WESTERN AUSTRALIA: King's Park, Perth (W. M. Wheeler).

NOTONCUS SPINISQUAMIS (André) new combination

Melophorus spinisquamis André, 1896, Rev. Ent., Caen, p. 254, worker, female, male. Type locality: Victorian Alps. Syntypes: Mus. Hist. Nat., Paris.

Diodontolepis spinisquamis, Wheeler, 1920, Psyche, **27:** 53. Clark, 1934, Mem. Nat. Mus. Victoria, Melbourne, **8:** 64. Wheeler, 1935, Psyche, **42:** 71.

Melophorus (*Melophorus*) *spinisquamis*, Emery, 1925, Genera Insect., **183:** 12.

This large, usually yellow or testaceous ant has very long legs and antennae, and the alitrunk is generally longer and more slender proportionately than in any of the other *Notoncus* species. In these same characters, *N. spinisquamis* also resembles *Aphaenogaster longiceps* (F. Smith), a common ant of the subfamily Myrmicinae with similar nocturnal habits and occupying the same localities.

The nest is usually or always built in the soil of moist or wet sclerophyll forest. Two nests I found in Sherbrooke Forest, Victoria, were under thick moss at the base of large *Eucalyptus regnans* trees, in a very wet, dark part of the forest. In each, only a handful of larvae and workers was found in what were probably only superficial chambers. I have seen other material from: VICTORIA: Millgrove; Beaconsfield; Belgrave (F. E. Wilson). Emerald (E. Jarvis). TASMANIA: King Island; Devonport (A. M. Lea). Isolated females from Victoria bear July and August dates.

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THE FOSSIL SALAMANDERS OF THE FAMILY SIRENIDAE

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No. 7—*The Fossil Salamanders of the Family Sirenidae*

By Coleman J. Goin and Walter Auffenberg

The Recent salamanders of the family Sirenidae comprise a rather compact group consisting of but two genera and three species. Their distribution is mainly restricted to the southeastern United States, although one species of *Siren* does reach Mexico. It is true that subspecies of the modern forms probably remain to be described, but the family can nonetheless be considered well known taxonomically in so far as Recent forms are concerned. On the other hand, although it has been known for nearly forty years that *Siren lacertina* occurred in the Pleistocene of Florida, their geologic history has remained practically unknown.

Our interest in the fossil sirenids goes back a number of years to the time when the senior author spent half a day with the late Clarence Simpson searching fruitlessly for fossil Sirenidae in the Florida State Geological Survey collection. Material has been slow to accumulate until recently when the junior author undertook a program of collecting the fossil snakes of Florida. Along with the snake material, occasional specimens of Sirenidae were discovered and these form the basis of this report.

So many small isolated deposits of Pleistocene material have been found in some localities, particularly near the village of Haile in western Alachua County, Florida, that it has been necessary for local collectors to refer to them by numbers. Where we have used these numbers to indicate the various deposits, we have given them in Roman numerals.

To facilitate comparisons of measurements of vertebrae of different sizes, in our type descriptions we have, in addition to the actual measurements in millimeters, also calculated each measurement in thousandths of the length of the centrum of that particular vertebra. These figures are given in parentheses following the measurements in millimeters. Unfortunately, the centrum is broken in the type of the Pliocene *Siren* so for it these calculations could not be made.

The two recognized genera of the Sirenidae are *Siren*, with

two Recent species, *lacertina* and *intermedia,* and *Pseudobranchus,* with a single Recent species, *striatus.* The former genus is larger in size and more widespread in distribution. In characters that can be recognized in fossil material, *Siren* differs from *Pseudobranchus* in that the lower margin of the centrum is nearly straight as seen from the side while in *Pseudobranchus* it is quite concave. Furthermore, in *Siren* the zygapophyseal ridge is gently curved or nearly straight and continues forward to meet the transverse process near the base of the prezygapophysis while in *Pseudobranchus* the ridge curves downward to meet and fuse with the transverse process in a shallow V posterior to the base of the prezygapophysis. In *Pseudobranchus* the zygapophyseal ridge has more of a tendency to flare where it fuses with the transverse process than it does in *Siren.*

Genus Siren

Siren lacertina Linnaeus

(Figures 1 and 3)

One striking thing about *lacertina* as compared to the other species of *Siren* is its large size; in this respect as well as in morphology the Pleistocene specimens are like *lacertina.* The vertebrae of *intermedia* are smaller but otherwise seem to be indistinguishable from those of *lacertina.*

This species has been known from the Pleistocene since Hay (1917) first recorded it from Stratum No. 3 from Vero, Indian River County, Florida. That it was widespread in Florida during the Pleistocene is shown by recently collected material, and we take this opportunity to summarize the fossil records known to us.

We have seen specimens from the following localities:

Florida, Alachua County
- Pit V, near Haile, NE 1/4, Section 23, R 17 E, T 9 S
- Pit IA, near Haile, SW 1/4, Section 24, R 17 E, T 9 S
- Pit VIIA, near Haile, SE 1/4, Section 24, R 17 E, T 9 S
- Pit IIB, near Haile, NW 1/4, Section 25, R 17 E, T 9 S
- Wall Company Pit, approximately 7 mi. W. of Gainesville, Section 35, R 18 E, T 9 S
- Pit IA, Kanapaha, Section 22, R 19 E, T 10 S

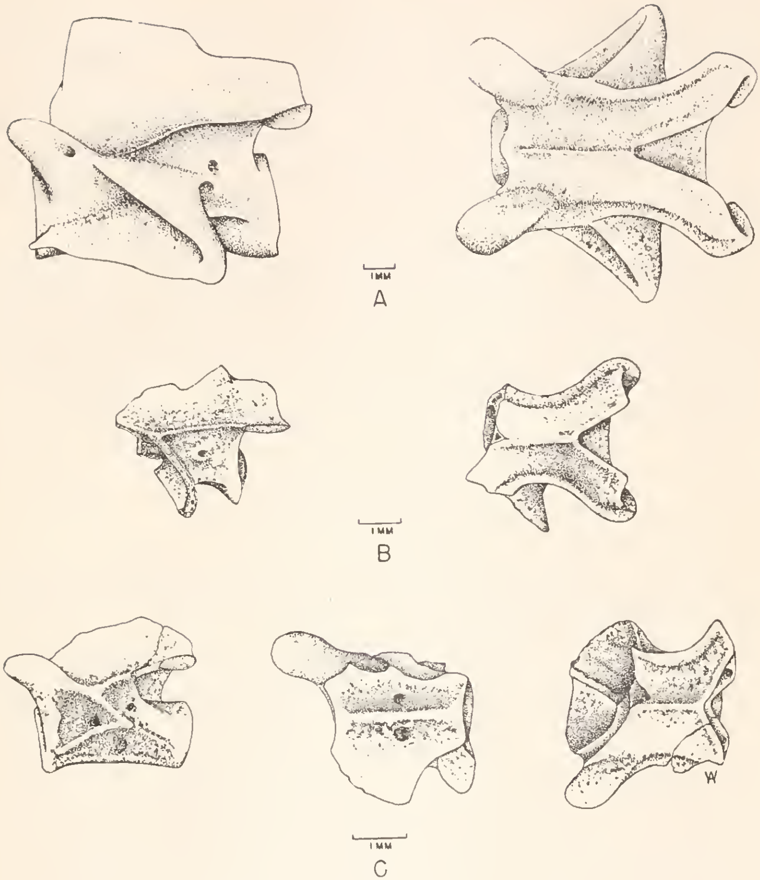

FIGURE 1

A. Lateral and dorsal views of thoracic vertebra of *Siren lacertina*. *B*. Lateral and dorsal views of *Siren simpsoni* sp. nov. Type, MCZ No. 2284. *C*. Lateral, ventral and dorsal views of *Siren hesterna* sp. nov. Type, MCZ No. 2278.

[1] Hornsby Springs, Section 27, R 17 E, T 7 S
Columbia County
[1] Ichtucknee Springs, Section 7, R 16 E, T 6 S
Indian River County
[1] Vero, Stratum No. 3
Marion County
1 mi. S. Reddick, Section 4, R 21 E, T 13 S
Brevard County
Melbourne

Several vertebrae of a *Siren* quite distinct from both *lacertina* and *intermedia* have been taken from a locality about four miles northeast of the town of Newberry, Alachua Co., Florida. The formation from which these specimens were taken is presumed to be Pliocene. We take pleasure in naming this species for our late friend, Clarence Simpson, who discovered this locality.

Siren simpsoni sp. nov.
(Figures 1 and 3)

Type. MCZ 2284, a thoracic vertebra.

Horizon and locality. Pliocene, Alachua Formation; Pit VI, SW 1/4, Section 24, R 17 E, T 9 S, a little south of the village of Haile, Alachua Co., Florida.

Referred material. Five thoracic vertebrae and a single second cervical vertebra (MCZ 2285) from the same locality as the type.

Diagnosis. A small *Siren* with the neural arch standing high above the centrum, a nearly straight zygapophyseal ridge as seen from the side and rather wide-flaring aliform processes. It can be distinguished from the Miocene species described below by the straighter zygapophyseal ridge as seen from the side and the smaller angle of the aliform processes. From *lacertina* and *intermedia* it can be distinguished by straighter zygapophyseal ridges as seen from the side and by the wider flare of the aliform processes.

Description of type. Measurements (in mm.): Width of vertebra at narrowest point of zygapophyseal ridges, 2.11. Angle between aliform processes, 62°. Height of anterior end of neural canal, 0.96. Angle of posterior edge of transverse process with axis of centrum, 85°.

[1] These deposits contain subfossil as well as Pleistocene material.

Lower half of centrum broken off, but the upper portion nearly intact. Centrum longer than high. Shape of ventral keel not determinable since it is broken off.

Total length of neural arch greater than length of centrum and its width at the narrowest portion of the zygapophyseal ridges slightly greater than width of centrum. Neural canal broken anteriorly; about rounded posteriorly; provided with a very low median epapophyseal ridge on the floor.

Articulating surfaces of prezygapophyses broken off. Articulating surfaces of postzygapophyses ovate. Zygapophyseal ridges well developed, markedly concave as seen from above. As seen from the side the zygapophyseal ridge is nearly straight and continues forward to near the base of the broken prezygapophysis.

Aliform processes well developed, vertical in position, somewhat rectangular as seen from the side. As seen from above they form an anteriorly pointing V. Floor between aliform processes present, with nearly straight posterior margin.

Neural spine well developed posteriorly; anteriorly it is broken off.

Transverse processes well developed and composed of two platelike portions. The ventral portion a wing-like structure extending from close to the anterior margin of the side of the centrum for about ¾ of the length of the centrum. The dorsal portion a flat plate extending from the zygapophyseal ridge somewhat behind the posterior margin of the prezygapophysis downward and backward to the posterior margin of the ventral portion to which it is fused. The posterior margin of the transverse process slants posteriorly. Laterally a foramen is present in the angle between the dorsal and ventral portions of the transverse process and another lies somewhat ventral and posterior to the angle between the dorsal portion of the transverse process and the zygapophyseal ridge.

Variation. The fragmented vertebrae that are referred to this species, in addition to the type, give some clues to variation. The body vertebrae and the cervical vertebra will be discussed separately.

Only two of the body vertebrae have the anterior neural canal complete; in these it is pentagonal in shape. In the one specimen that has adequate zygapophyseal ridges they are not quite so concave as seen from above as they are in the type. The single

specimen in which the aliform processes are discernible has them at about the same angle as does the type. The upper portion of the transverse process meets the zygapophyseal ridge in about the same place as in the type in two specimens and slightly posterior to that point in two others.

The second cervical vertebra mentioned above differs from those of recent species of *Siren* in several respects. The neural arch stands much higher above the centrum and the total height of the vertebra is about a fourth again greater than the length of the centrum whereas in the recent species the height of the vertebra is about equal to the length of the centrum. This difference is reflected in the anterior aspect of the neural canal which in *simpsoni* is higher than wide while in *lacertina* it is wider than high. Furthermore, *simpsoni* has much shorter aliform processes than do the recent species. In this vertebra in *simpsoni* each aliform process is shorter than the neural spine, while in *lacertina* the neural spine is shorter than either of the aliform processes.

All of the specimens of *simpsoni* are broken to a greater or less degree while the specimens of *Pseudobranchus* from the same deposit are more or less intact. This is possibly due simply to the relative size of the two genera since the same condition obtains in snakes from this deposit where again we find the vertebrae of small species largely intact while those of the larger species are apt to be broken.

Locality and associated fauna. The site from which these fossils were taken is about 0.2 miles east of State Highway 235, near the village of Haile, Alachua Co., Florida. The elevation is about 84 feet.

The deposit was exposed during construction of a roadbed for a railroad spur to a commercial limestone quarry. Workmen noticed fossils in the deposit and forwarded them to Clarence Simpson who recognized the association as a non-marine Pliocene one. Mr. Simpson started preliminary excavation but time did not permit him to study the deposit thoroughly before his untimely death. Fortunately, however, he did show Professor A. S. Romer the site and it was at Professor Romer's suggestion that the junior author reopened the deposit for further study.

The upper stratum at this locality has been modified by the construction of the adjoining roadbed. In places where this

stratum has not been disturbed it consists of grayish, unconsolidated sands several feet in thickness. In the spot where the fossiliferous clay was originally exposed, subsequent deposition from the adjoining roadbed has covered the clay with a thin, sandy, grass-covered mantle containing such artifacts as cinders and even rusty nails.

Test borings indicate that the clay bed is approximately thirty feet in diameter and that laterally it grades into a yellowish sandy material that has not been examined for fossils.

The stratigraphy is as follows:

3. A recently modified sandy stratum, containing artifacts of construction . . . . 0-1′

2. A faintly bedded, yellowish to brownish sandy clay, weathering to reddish brown on exposure, containing very thin lenses of a plastic grayish clay. Small, polished phosphatic pebbles and boulders composed of cemented grayish phosphatic sands and darker pebbles, as well as smoothly eroded boulders of highly silicified Ocala Limestone are common. Laterally this bed grades into yellow or yellowish brown sands with little clay . . . . 1-7′

1. Ocala Limestone.

Remains of a horse, *Hipparion* cf. *minor*, suggest a Pliocene age for the fauna that is found in stratum 2. These clays of stratum 2 apparently represent a fresh water deposit. Several aquatic snakes and a turtle of the genus *Pseudemys,* as well as *S. simpsoni*, occur here. The turtle seems referable to *Pseudemys caelata* Hay, a species definitely associated with a Pliocene fauna at the Mixson locality which lies two miles northeast of Williston, Alachua Co., Florida, and is the type locality of the Alachua Formation. The snakes, still mostly undescribed, and the *Siren* are definitely different from the snakes and *Siren* of the well known Pleistocene localities in Florida and also differ from the snakes and *Siren* of the Lower Miocene of the Thomas Farm.

A single vertebra of a *Siren* from the Miocene was found in a bag of loose matrix taken from the boulder bar in the pit at the Raeford Thomas Farm in Gilchrist County, Florida. This local-

ity has been described in detail by White (1942). This species differs from the one described above and from the two Recent species.

Siren hesterna sp. nov.

(Figure 1,*C*)

Type. MCZ 2278, a posterior thoracic vertebra.

Horizon and locality. L. Miocene, Arikareean; Raeford Thomas Farm, Gilchrist Co., Florida.

Diagnosis. A small *Siren* with strongly diverging zygapophyses, with a high neural arch, and with a very wide angle (123°) between the aliform processes. The forward sweeping posterior margin of the transverse process and the widely diverging aliform processes serve to distinguish it from *lacertina, intermedia* and *simpsoni*.

Description of type. Measurements (in mm.): Length of centrum along midventral line, 2.67. Narrowest width of zygapophyseal ridges, 2.3 (.861). Height of vertebra from lower margin of centrum to a line drawn between facets of postzygapophyses, 2.06 (.772). Angle between aliform processes, 123°. Angle of posterior edge of transverse process with axis of centrum, 120°.

Centrum longer than high; posterior glenoid cavity oval to round. Centrum provided with a median ventral keel, on either side of which is found a single, relatively large, subcentral foramen. Margin of ventral keel nearly straight.

Total length of neural arch greater than length of centrum and its width at the narrowest portion of the zygapophyseal ridges slightly greater than width of centrum. Neural canal about rounded posteriorly; without a well developed median epapophyseal ridge on the floor.

Articulating surfaces of prezygapophyses oval in shape, longer than wide, directed more anteriorly than laterally. Their greatest length 1.8 (.674). Articulating surfaces of postzygapophyses broken. Zygapophyseal ridges well developed, markedly concave as seen from above. As seen from the side the zygapophyseal ridge is nearly straight but slants downward anteriorly, meeting the transverse process near the base of the prezygapophysis.

Aliform processes well developed, vertical in position, somewhat rectangular as seen from the side. As seen from above they form an anteriorly pointing V. Floor between aliform processes present but with posterior margin eroded.

Neural spine well developed but its margin eroded so that its form is indeterminable.

Transverse processes well developed and composed of two platelike portions, of which the ventral seems to be larger than the dorsal. The ventral portion is a winglike structure extending from the anterior margin of the side of the centrum for about ¾ of the length of the centrum. The dorsal portion is a flat plate extending from the posterior margin of the prezygapophysis downward and backward to the posterior margin of the ventral portion to which it is fused. Transverse process as well as can be determined slants upward from the horizontal. Laterally a foramen is present in the angle between the dorsal and ventral portions of the transverse process and another lies between the dorsal portion of the transverse process and the zygapophyseal ridge.

Genus Pseudobranchus

A species of *Pseudobranchus* with large and robust vertebrae has been collected at two Pleistocene localities in Alachua County.

Pseudobranchus robustus sp. nov.

(Figure 2,*B*)

Type. MCZ 2279, a middle thoracic vertebra.

Horizon and locality. Pleistocene; Pit VIIA, SE ¼, Section 24, R 17 E, T 9 S, a little south of the village of Haile, Alachua Co., Florida.

Referred material. Five vertebrae (MCZ 2280) from the same locality as the type and a single vertebra (MCZ 2281) from the Pleistocene at Kanapaha, Pit 1A, Section 22, R 19 E, T 10 S, in Alachua County, Florida.

Diagnosis. A *Pseudobranchus* with large, massive articulating facets on the zygapophyses and with the margins of the zyga-

pophyseal ridges pronouncedly concave as seen from above. It differs from the modern species in the wider angle between the aliform processes and in the more concave sides of the zygapophyseal ridges as seen from above. From the Pliocene species described below it differs in the stronger concavity of the zygapophyseal ridges and in the more widely flaring, relatively shorter aliform processes.

Description of type. Measurements (in mm.): length of centrum along midventral line, 2.36. Width of vertebra at narrowest point of zygapophyseal ridges, 1.11 (.470). Height of vertebra from lower margin of centrum to a line drawn between facets of postzygapophyses, 1.31 (.555). Distance between outer edges of prezygapophyses, 2.21 (.936). Distance from tips of prezygapophyses to tips of postzygapophyses, 3.08 (1.305). Angle between aliform processes, 81°. Width of anterior glenoid cavity, 1.20 (.508); height of anterior glenoid cavity, 0.89 (.377). Width of neural canal, 0.86 (.364); height of neural canal, 0.53 (.225). Angle of posterior edge of transverse process with axis of centrum, 90°.

Centrum longer than high; glenoid cavity oval, wider than high. Centrum provided with an elevated, ridge-like, median ventral keel, on either side of which is found a relatively large, subcentral foramen. Margin of ventral keel pronouncedly concave.

Total length of neural arch greater than length of centrum and its width at the narrowest portion of the zygapophyseal ridges slightly greater than width of centrum. Neural canal an inverted crescent anteriorly; about rounded posteriorly; provided with a very low median epapophyseal ridge on the floor.

Articulating surfaces of prezygapophyses oval in shape, longer than wide, directed more anteriorly than laterally. Articulating surfaces of postzygapophyses ovate. Zygapophyseal ridges well developed, markedly concave as seen from above. As seen from the side the zygapophyseal ridge forms a very shallow V with the apex at the point where the dorsal portion of the transverse process meets the zygapophyseal ridge.

Aliform processes well developed, vertical in position, somewhat rectangular as seen from the side but the left one somewhat eroded. As seen from above they form an anteriorly pointing V. Floor between aliform processes present, with nearly straight

posterior margin.

Neural spine well developed, but dorsal margin broken.

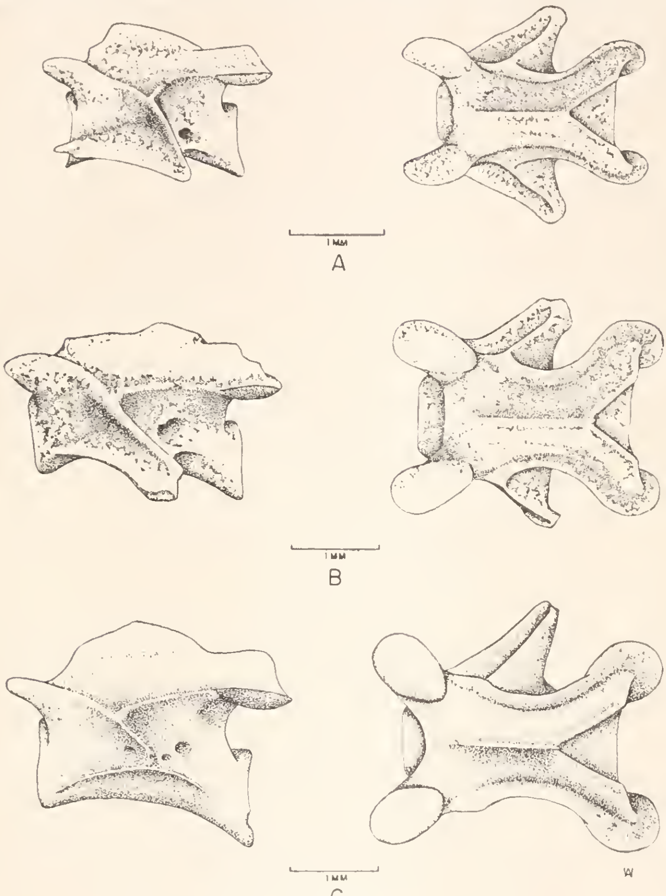

FIGURE 2

A, Lateral and dorsal views of thoracic vertebra of *Pseudobranchus s. axanthus*. *B*, Lateral and dorsal views of *Pseudobranchus robustus* sp. nov. Type MCZ No. 2279. *C*, Lateral and dorsal views of *Pseudobranchus vetustus* sp. nov. Type, MCZ No. 2282.

Transverse processes well developed and composed of two platelike portions, of which the ventral is larger than the dorsal.

The ventral portion a wing-like structure extending from close to the anterior margin of the side of the centrum for about 4/5 of the length of the centrum. The dorsal portion a flat plate extending from the zygapophyseal ridge somewhat behind the posterior margin of the prezygapophysis ventrally and posteriorly to the posterior margin of the ventral portion to which it is fused. The posterior margin of the transverse process is approximately perpendicular to the axis of the centrum. Laterally a foramen is present in the angle between the dorsal and ventral portions of the transverse process and another lies somewhat ventral and posterior to the angle between the dorsal portion of the transverse process and the zygapophyseal ridge.

Variation. The six vertebrae referred to this new species in addition to the type are remarkably constant in specific characters, and most of the variation seems due to erosion or to fragmentation. They all have wide-flaring aliform processes and they all have the zygapophyseal ridges pronouncedly concave as seen from above. In them the same massive structure so apparent in the type is characteristic. Without exception the dorsal portion of the transverse process fuses with the zygapophyseal ridge posterior to the base of the prezygapophysis and the angle of the zygapophyseal ridge where it meets the dorsal portion of the transverse process is about the same as it is in the type and definitely more obtuse than it is in *striatus*. One of the vertebrae must have been from the very anterior portion of the thorax since a double articulation for a two-headed rib can be seen on the tip of the transverse process. The most pronounced variation discernible in these six vertebrae is in the margin of the median subventral keel. In four of them it is quite concave, as in the type of *P. robustus* and in modern *P. striatus*, but in one of them the curve is more reduced. In the sixth specimen the centrum is fractured. The massiveness of the vertebrae, the large size of the articulating facets, and the pronounced concavity of the zygapophyseal ridges are as characteristic of these six vertebrae as of the type.

Locality and associated fauna. The site from which the type was taken is on the north end of a large limestone pit about 0.5 miles east of State Highway 235, near the village of Haile, Alachua County, Florida. The elevation is about 84 feet.

The stratigraphy is as follows:

4. A reddish-brown sandy clay containing few fossils 0-3′±
3. A complex stratum composed of many intergrading lenses of whitish sands, brownish sands, numerous bits of eroded Ocala limestone, grayish sandy clays, etc. . . . . 3-7′±
2. A bedded, bluish to bluish gray clay forming the lowest layer of the deposit . . . . . 7-15′±
1. Ocala Limestone

The presence of *Equus, Dasypus bellus, Holmesina* and *Testudo sellardsi* indicate the Pleistocene age of the fauna. The general structure of the formation suggests that it was laid down in a sink hole pond and the presence of *Pseudobranchus, Siren lacertina, Alligator, Pseudemys* and *Natrix* may be considered indicative of a pond fauna. The *Pseudobranchus* was collected from Stratum 3.

An undescribed species of *Pseudobranchus* was found in the same Pliocene deposit in which *Siren simpsoni* was found. For this new *Pseudobranchus* we propose the name

PSEUDOBRANCHUS VETUSTUS sp. nov.

(Figure 2,*C*)

Type. MCZ 2282, a thoracic vertebra.

Horizon and locality. Pliocene, Alachua Formation; Pit VI, SW ¼, Section 24, R 17 E, T 9 S, a little south of the village of Haile, Alachua Co., Florida.

Referred material. Six vertebrae (MCZ 2283) from the same locality as the type.

Diagnosis. A *Pseudobranchus* in which the neural arch stands high on the centrum. It differs from *robustus* in the less concave zygapophyseal ridges as seen from above and in the reduced angle between the aliform processes. From the Recent species it differs in having a higher neural arch.

Description of type. Measurements (in mm.): Length of centrum along midventral line, 2.36. Width of vertebra at narrowest point of zygapophyseal ridges 1.46 (.619). Height of vertebra from lower margin of centrum to a line drawn between facets of postzygapophyses, 1.53 (.648). Distance between outer edges of prezygapophyses, 2.10 (.890). Distance from tips of prezyga-

pophyses to tips of postzygapophyses, 3.26 (1.381). Angle between aliform processes, 57°. Width of anterior glenoid cavity, 0.89 (.377); height of anterior glenoid cavity, 0.94 (.398). Width of neural canal, 1.14 (.483); height of neural canal 0.69 (.292). Angle of posterior edge of transverse process with axis of centrum, 78°.

Centrum longer than high; glenoid cavity round. Centrum provided with an elevated, ridge-like, median ventral keel, on either side of which is found a relatively large, subcentral foramen. Margin of ventral keel pronouncedly concave.

Total length of neural arch greater than length of centrum and its width at the narrowest portion of the zygapophyseal ridges slightly greater than width of centrum. Neural canal pentagonal, wider than high; about rounded posteriorly; provided with a very low median epapophyseal ridge on the floor.

Articulating surfaces of prezygapophyses oval in shape, longer than wide, directed more anteriorly than laterally. Articulating surfaces of postzygapophyses ovate. Zygapophyseal ridges well developed, markedly concave as seen from above. As seen from the side the zygapophyseal ridge forms a very shallow V with the apex at the point where the dorsal portion of the transverse process meets the zygapophyseal ridge.

Aliform processes well developed, vertical in position, somewhat rectangular as seen from the side. As seen from above they form an anteriorly pointing V. Floor between aliform processes present, with concave posterior margin.

Neural spine well developed.

Transverse processes well developed and composed of two platelike portions of which the ventral is larger than the dorsal. The ventral portion a wing-like structure extending from the anterior margin of the side of the centrum for about ⅔ of the length of the centrum. The dorsal portion a flat plate extending from a point on the zygapophyseal ridge somewhat posterior to the posterior margin of the prezygapophysis ventrally and posteriorly to the posterior margin of the ventral portion to which it is fused. The posterior margin of the transverse process is not quite perpendicular to the axis of the centrum. Laterally a foramen is present in the angle between the dorsal and ventral portions of the transverse process and another lies somewhat posterior and ventral to the angle between the dorsal portion of

the transverse process and the zygapophyseal ridge.

Variation. The six vertebrae referred to this new species in addition to the type seem constant in specific characters. The flare of the aliform processes is similar to that in the type and the zygapophyseal ridges show about the same degree of concavity as seen from above, except in two which are apparently from the anterior portion of the body. In these two the sides are more nearly straight. The anterior articulating facets are similar to those of the type; in three of the five which have good posterior articulating facets, they are slightly narrower and longer than they are in the type. The point of fusion between the dorsal portion of the transverse process and the zygapophyseal ridge is similar to the type in five out of six. In the other, a more anterior vertebra, the transverse process joins the zygapophyseal ridge near the base of the prezygapophysis. The degree of concavity of the median subventral keel is similar to the type in three specimens, but in two it is more nearly straight; in one the margin is broken. Two out of the six have the aliform processes not so high as in the type and other four specimens. In the one specimen that has a complete neural spine, the spine is highest anteriorly and the anterior margin is practically vertical.

Evolutionary Trends

Several general trends can be noted in the evolutionary history of the Sirenidae. In the genus *Siren* there is a pronounced tendency for the angle between the aliform processes to be reduced with time. *S. hesterna* of the Miocene has the widest angle and the two Recent species have the smallest. Correlated with this there is an elongation of the aliform process in relation to the length of the neural spine. It seems that the change is simply a transposition forward of the apex of the angle where the aliform processes meet, resulting in a reduction of the angle between them, a lengthening of the aliform processes and a reduction in the length of the neural spine all at the same time.

Another trend seems to be the reduction in the height of the neural arch, with the arch of *hesterna* standing highest above the centrum and that of the Recent species the lowest.

The latter tendency occurred in the genus *Pseudobranchus* from the Pliocene to the present day species although it is not

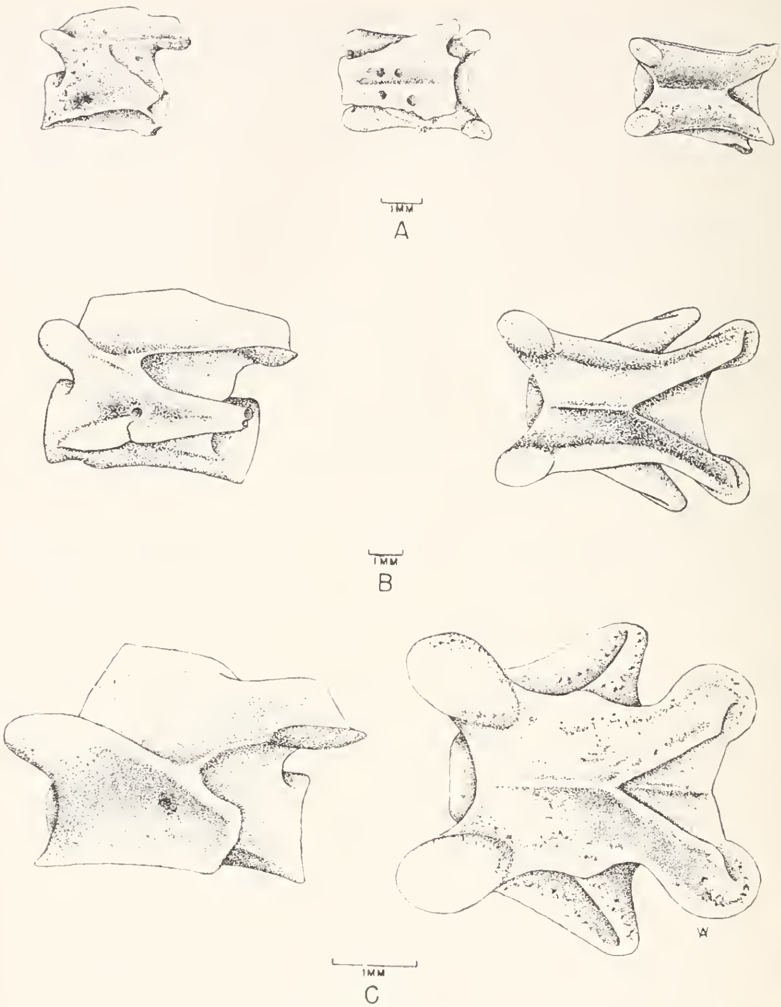

FIGURE 3

A, Lateral, ventral and dorsal views of second cervical vertebra of *Siren simpsoni. B,* Lateral and dorsal views of second cervical vertebra of *Siren lacertina. C,* Lateral and dorsal views of thoracic vertebra of *Pseudobranchus s. striatus.*

so pronounced in this genus as in *Siren*.

The presence of both genera in the same deposit in the Pliocene gives assurance that the two genera must have become separate at some earlier date. This need not be projected backward very far however, for *P. vetustus* of the Pliocene is much more *Siren*-like than any of the more Recent forms of the genus and this may indicate that at that time they had not been too long separated.

The most obvious single evolutionary step is the large size attained by *lacertina* in the Pleistocene. All the other species are small, as small as or smaller than Recent *intermedia* from Florida. The earliest known *Siren* was thus a small, *intermedia*-like species and the line of small forms continues from the Miocene to the present, with the large *lacertina* probably derived from this line during the early Pleistocene. Thus the Sirenidae, like so many other groups, has a Pleistocene representative that exhibited a saltatorial increase in size.

In the genus *Pseudobranchus*, the well known form *axanthus* and the poorly known *striatus*, which has not even been collected in recent decades, have been considered as races of a single species, primarily on geographic grounds. However, there is enough divergence in the vertebrae of these two forms to deserve special comment. *P. s. striatus* has a heavier, more robust vertebra than does *axanthus* and in addition it has a low, median ridge on the floor between the aliform processes. While there may be no reason that differences of this sort could not occur between two subspecies of a single species, they do suggest that it might be worth while to reinvestigate the status of these two forms when material from the appropriate localities becomes available. The vertebrae of *P. s. spheniscus* we have examined, while exhibiting minor differences, seem to be essentially similar to those of *axanthus* rather than to those of *striatus*.

Table 1 gives a summary of the distribution of the Sirenidae in time as we now know it.

Table 1

Recent	*Siren lacertina* *Siren intermedia* (2 described subspecies, *intermedia* and *nettingi*) *Pseudobranchus striatus* (5 described subspecies, *striatus*, *axanthus*, *spheniscus*, *lustricolus*, and *belli*)
Pleistocene	*Siren lacertina* *Pseudobranchus robustus*
Pliocene	*Siren simpsoni* *Pseudobranchus vetustus*
Miocene	*Siren hesterna*

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